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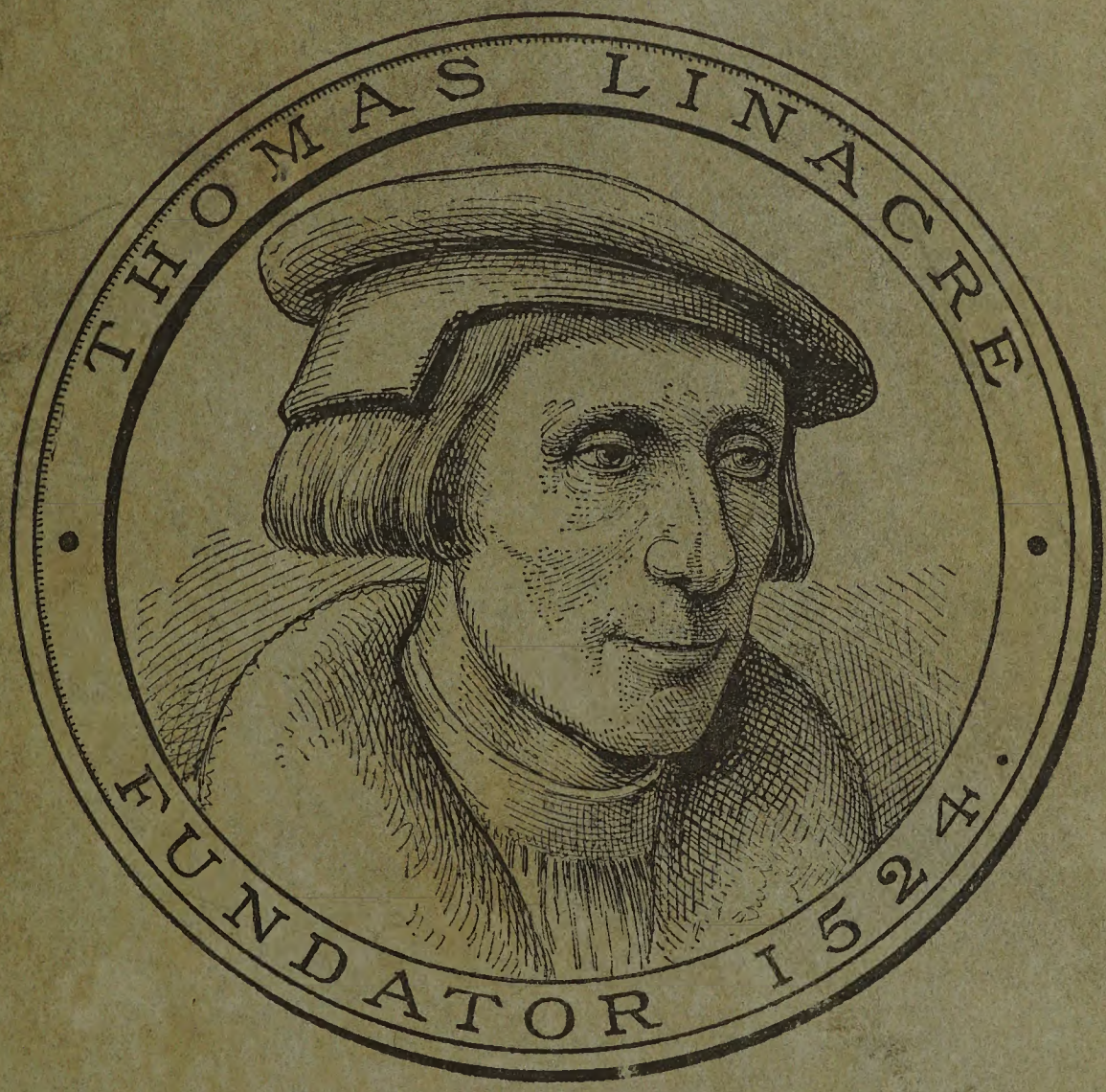

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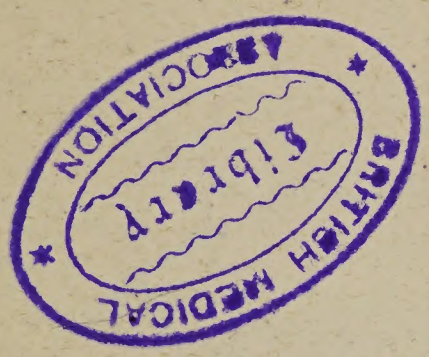

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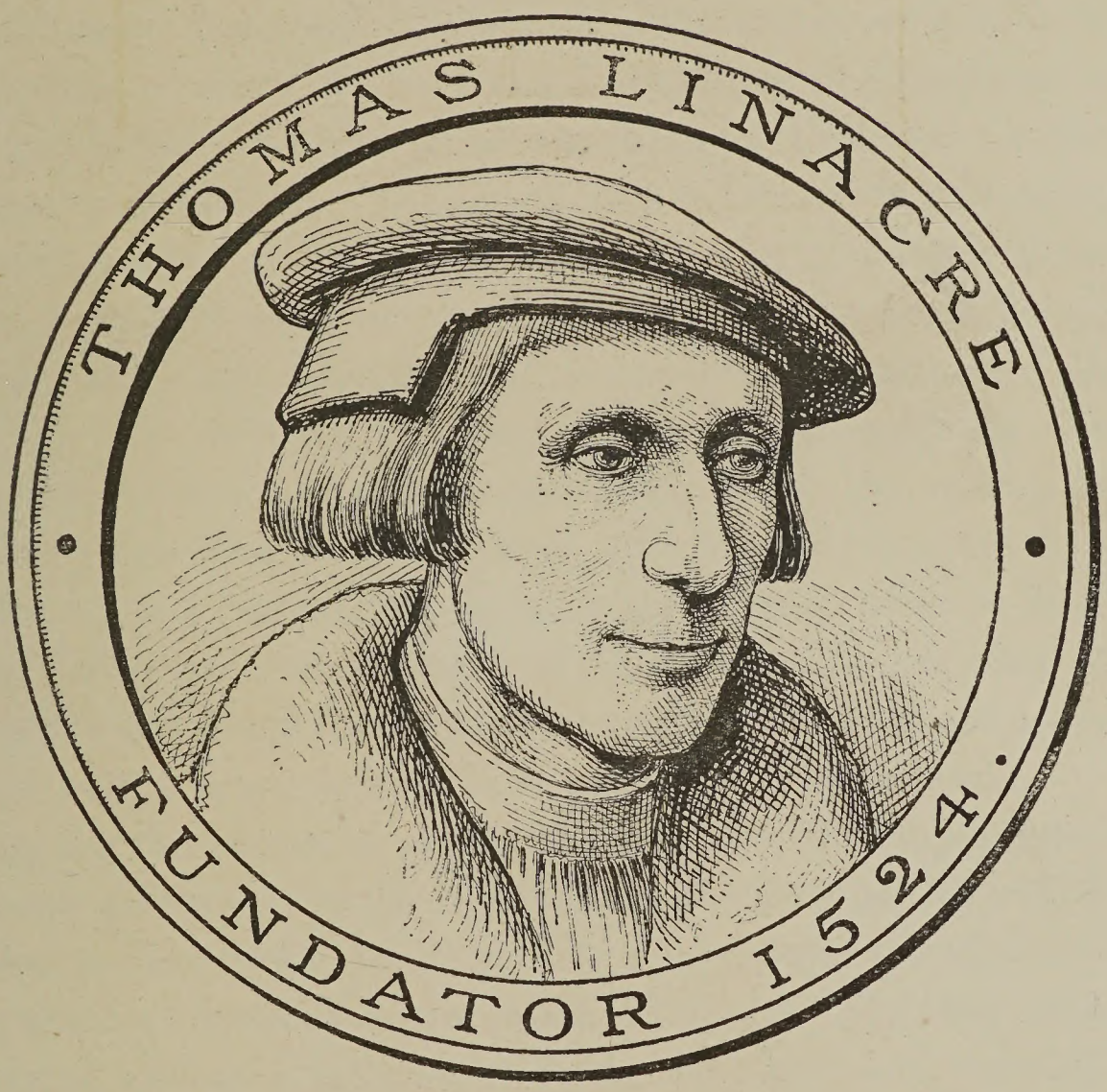

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PREFACE.

I PROPOSE to issue from time to time, under the title of 'The Linacre Reports,' reprints of publications setting forth the results of work done in the Laboratory of Comparative Anatomy under the charge of the Linacre Professor in the University of Oxford. The object I have in view in collecting the publications of my pupils and colleagues is to place them in the hands of members of the University who are not conversant with the literature of Comparative Anatomy. In this way the evidence is offered that the laboratories and collections under my charge are being made the means of producing new knowledge. Those who believe that the production of new knowledge is at least as important a duty of the University and Colleges of Oxford as the training of youths for the competitions of the examination room and playground will, I hope, find in these pages some satisfaction.

They are the result, or part of the result, of the employment of money generously voted by students of historical and other sciences to furnish and maintain the workshop of the students of the science known as Comparative Anatomy. They are but a first crop, and give promise of more abundant and weighty fruit in the future.

The memoirs contained in this collection represent work done in the years 1891, 1892, and the earlier part of 1893. They are sixteen in number, and treat of various groups of the animal kingdom, from the microscopic Protozoa to the extinct Mammalia of the Oxford oolite. Owing to my illness during Michaelmas term, 1892, one memoir which should be

in the collection was not ordered for reprint, namely, that by Dr. Benham on a very interesting new worm from the Thames near Oxford, to which he has given the name Sparganophilus ('Quart. Journ. Micr. Sci.,' vol. xxxiv, November, 1892).

Some of the researches here recorded have been undertaken in the laboratory upon material expressly collected, whilst others are the result of the careful examination and arrangement of the valuable collections placed in the University Museum. My share in the matter has been confined to giving such help as I could in procuring material or suggesting an inquiry; and in the case of less experienced workers offering occasional advice, which has been always kindly recorded.

In a future volume of these 'Reports' will be included the results of work done in 1893, but not yet published, namely, by Mr. Gilbert Bourne, M.A., of New College, on the life-history of the Coral Fungia, by Mr. R. T. Günther, of Magdalen College, on the structure of the two fresh-water Medusæ, Limnocodium and Limnocnida (the latter described by him in No. 9 of the present collection), by Dr. Benham on the brain of the chimpanzee "Sally," lately deceased in the Zoological Gardens, London, and by Miss Gould on the structure of the Protozoon Pelomyxa.

The medallion portrait which is printed on the title-page of this volume has been drawn from a photograph of the oil painting of Linacre in the rooms of the Royal College of Physicians of London. My thanks are due to my friend Dr. Frank Payne for the loan of the photograph.

E. RAY LANKESTER.

Oxford; January 8th, 1894.

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3. On a Sieve-like Membrane across the Oscula of a Species of Leucosolenia, with some Observations on the Histology of the Sponge, by Edward A. Minchin, M.A., Fellow of Merton College. (From the 'Quarterly Journal of Microscopical Science,' vol. xxxiii, January, 1892.)

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6. The Oscula and Anatomy of Leucosolenia clathrus, O. S., by E. A. Minchin. (From the 'Quarterly Journal of Microscopical Science,' vol. xxxiii, June, 1892.)

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8. A New Sporozoon in Amphioxus, by E. C. Pollard, B.Sc., Somerville Hall. (From the 'Quarterly Journal of Microscopical Science,' vol. xxxiv, January, 1893.)

9. Preliminary Account of the Fresh-water Medusa of Lake Tanganyika, by R. T. Günther, B.A., Magdalen College. (From the 'Annals and Magazine of Natural History,' series 6, vol. xi, April, 1893.)

10. Description of a New Species of Moniligaster from India, by W. B. Benham. (From the 'Quarterly Journal of Microscopical Science,' vol. xxxiv, April, 1893.)

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17. On the Fossil Mammalia from the Stonesfield Slate, by E. S. Goodrich. (From the 'Quarterly Journal of Microscopical Science, vol. 35, January, 1894.)

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Notes on some Aquatic Oligochæta.

By

W. Blaxland Benham, D.Sc.Lond.,
Aldrichian Demonstrator of Comparative Anatomy, Oxford.

With Plates V, VI, and VII.

Contents.

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7. Supposed constancy of *n* in species of Nais, p. 213.

During the present spring (1891) I had under observation at various times a number of aquatic Oligochæta, for the purpose of illustrating my lectures to the students here who were working at the group; and I came across several interesting facts, some of which are worth recording in these pages.

Wishing to obtain examples of Oligochæta living on the sea-shore, I wrote to Mr. W. H. Shrubsole, of Sheerness, and he was good enough to obtain for me several gatherings from the neighbourhood. I wish to convey to him my best thanks for the energy and promptness which he displayed in acceding to my requests.

Amongst these gatherings, living in dark, smelling, decaying organic detritus, I found Hemitubifex ater, Paranais littoralis, Clitellio arenarius, and Pachydrilus sp., together with a worm originally diagnosed very briefly by Claparède about thirty years ago, which appears to have

escaped the notice of naturalists since that time. To it he gave the name Heterochæta costata; the generic name referring to the interesting arrangement of chætæ, and the specific to longitudinal ridges, or to the distinctly annulate character of the segments.

Of these worms I found abundant specimens in some of the earlier gatherings (in May); but more recently, in the latter end of June, I have been able to find only a few specimens, though I still find a few fully mature forms now in July.

Heterochæta costata, Claparède, 1863.

In his studies on Invertebrates from the coast of Normandy ('Beobach. u. Anat. und Entwickel. wirbellöser Thiere') Claparède gives (p. 25) a brief diagnosis of a new genus, of which the following is a translation:

"Heterochæta, n. gen.

"Chætæ bundles in two rows (on each side); those of the upper row, on Segments v to viii, are hollowed out at the free end in the form of a cup. The remaining chætæ are all crotchet-shaped [hakenförmig].

"H. costata, n. sp., Taf. xiii, figs. 16 to 19.

"Body 16 mm. in length, $\frac{1}{2}$ mm. in breadth; skin ribbed by longitudinal grooves; each segment divided into rings by about four constrictions."

He further states, during a brief extension of the diagnosis, occupying only eight lines, that all his specimens were immature and without a clitellum; that the peculiar chætæ (which he figures) have a constriction just below the cup (or "becher"); that the ordinary chæta has a swelling (or "node," as I will call it) about midway along its length. The vascular system consists of a dorsal vessel, a ventral vessel, and a loop in each of the hinder segments.

This is essentially all that is known of this interesting worm;

and Vejdovsky makes no remarks upon it, merely giving Claparède's diagnosis almost textually ('System und Morph. d. Oligochæta,' p. 84). Vaillant, in the 'Hist. nat. d. Annélides,' has no more to say of it.

In the above diagnosis there is one error, which I will point out at once. The chætæ referred to as "becherförmig" are not cupped; they are what is known as fan-shaped (or palmate, as I shall call them), such as are characteristically found in Psammoryctes.

I have been able to extend our knowledge of this worm, and will now give my own observations on Heterochæta.

During life the worm is pink in colour, the sperm-sacs and ova in mature animals showing up white.

The length is about five eighths of an inch when fully mature, and exceptionally slightly longer; but I have seen none that attain a length of one inch. The white region which marks the position of the genital cells occupies about one eighth of an inch, commencing about the same distance from the anterior end (fig. 1). The number of segments is about forty.

In habit it resembles Hemitubifex, &c., amongst which it lives; and I found it sometimes by itself in the mud, with posterior end protruded therefrom, as is the habit of other members of the family, or twisted and coiled amongst the Hemitubifex in the "balls" which the latter form.

When disturbed, an individual will roll itself into a spiral, or twist itself into a knot (fig. 2).

It is not by any means easy to distinguish Heterochæta by the naked eye from such forms as Paranais littoralis, Pachydrilus, or even some paler forms of Hemitubifex. I have found it impossible to identify them without picking them out and using a low-power microscope for their examination; and even then, unless they happen to present their dorsal surface to view, it requires great practice to appreciate the exact shade of pink which serves to distinguish them from the other worms mentioned above.

If, however, the back is uppermost, then one can readily

recognise the fan-shaped bundles of dark palmate chætæ on Segments v to xiii [1] (fig. 3).

The ventral chætæ (figs. 12, 13) are practically all alike, to wit, crotchets or "furcate" chætæ; although the size of the prongs and the angle between may vary in different parts of the body. The dorsal chætæ, with the exception of those on Somites v to xiii (both inclusive), are similar to the ventral chætæ. These are shown in figs. 10, 11.

The dorsal chætæ of Segments ii, iii, iv, have the two prongs very nearly equal, the lower (or proximal) prong being slightly smaller than the upper or distal prong; the two prongs are not greatly divergent (fig. 10). The dorsal chætæ of the hinder segments are slightly stronger than the anterior ones; the proximal prong is shorter than the distal prong, and has a decided curve away from the latter, so that the angle between them is slightly more obtuse than that of the anterior dorsal chætæ (fig. 11).

The ventral chætæ present a similar difference according to their position—namely, those of the more anterior segments (fig. 12) have less divergent prongs than have those of the more posterior segments (fig. 13); and there is the same difference in size of the prongs as occurs in the dorsal bundles. These differences agree with those figured by Professor Lankester for Psammoryctes umbellifer ('Ann. Mag. Nat. Hist.,' 4th ser., vii, 1871, p. 92). Similar differences have been noticed in other members of the family Tubificidæ.

The dorsal chætæ of Segments v to xiii closely agree in appearance with those described and figured by Lankester as characteristic of Psammoryctes umbellifer; where they occur, however, in Segments ii to x.

Each of these palmate chætæ has the appearance presented by fig. 4. The stalk or axis of the chæta is straight, swollen at the point where it passes through the skin in a protruded

[1] The numeration that I here adopt is that usually followed by recent writers on Oligochæte anatomy—namely, to regard the first chætigerous segment as the second [ii] body-segment; the buccal or peristomial segment being the first [i] segment.

state; then narrows, as Claparède stated, before dilating to form the "head."

This "head" is flattened from in front backwards in the natural position of the chæta as seen in a living worm, and expanded laterally; it is not cup-shaped: this appearance is an optical illusion. When seen from in front this head is seen to be formed by seven or eight blunt teeth; and each is slightly curved forwards, so that the free edge of each "tooth" is marked by a thicker line. The "teeth" appear at first sight to be separated from one another by very fine spaces, but I believe these spaces are in reality occupied by an extremely thin transparent membrane, as in Psammoryctes and Tubifex.

I was at first inclined to regard the "teeth" as separate from one another; but, as Professor Lankester remarked to me, if this were so, the lines between the "teeth" would appear much more pronounced, owing to refraction along the edges, than is the case.

And further observation served to assure me that there is such a membrane; it can be distinguished by the use of Zeiss's homogeneous immersion, with compensating eye-piece 4. Moreover if the chætæ, during the movements of the bundles to and fro, be looked at from above (with a Zeiss' E, and No. 2 eye-piece), so that the free edge only of the structure be seen in focus, we get a curved beaded appearance (fig. 7); the thicker parts are the "teeth," the thinner are the intervening membranes. This interpretation is further confirmed by a very lucky find of an abnormal variety of the chæta, in which the "teeth" are scarcely differentiated, and we have a continuous membrane with extremely faint lines across it (fig. 9). This is not a young chæta, but occurred in middle of a bundle of palmate chætæ, and was of same size as these.

The whole of the "head" is curved at its sides, as shown in fig. 7, and at the same time is bent forwards, as in fig. 6. Hence the whole "head" can never be in focus at one and the same time under a high power. This leads to the appearance represented in fig. 5, where the two most laterally placed or outer teeth or ridges are in focus, whilst the remainder are

only imperfectly focussed; hence the outermost ridges appear more strongly defined than the rest (see Lankester's and Vejdovsky's figures of Psammoryctes), but by careful focussing it appears to me that all the ridges are equally developed.

Now, if one of these chætæ be observed from above during life, so that we look down it, we shall of course see the head foreshortened, and we have the appearance portrayed in fig. 8. This has somewhat the appearance of a cup, one side of the cup being formed by the free edge of the teeth, whilst the two outer ridges and the thick stalk immediately below the head form the curve which may be mistaken for the other side of the cup; and I believe this appearance deceived Claparède. These palmate chætæ vary in number on different segments, as the following table and fig. 3 show; there is also individual variability for each bundle.[1] The chætæ of a bundle, when in movement, diverge from one another in a fan-shaped manner, the edges of the various chætæ almost touch, and are so regularly arranged as to form part of a curve. The whole bundle is moved backwards and forwards—striking the water, that is to say, with the flat faces of the chætæ, which no doubt serve as oars. It is interesting to note that the furcate chætæ are freqnently rotated on their own axes, in addition to their to and fro movement; and that not unfrequently the angle between the prongs, which is normally directed downwards, is directed upwards. There appears to be a much greater freedom of movement in all directions in the furcate bundles than in the palmate bundles.

Although these facts can be to a very great extent observed in a living worm, slightly compressed by a cover-glass to prevent too active a movement, yet it is necessary, in order to properly ascertain the character of the chætæ, to treat them with caustic potash. This I did, and have mounted them in glycerine jelly, which, as Professor Lankester has observed, is a most useful mounting medium for chætæ.

When treated with KHO, however, the embedded ends of

[1] That is, the bundle of the corresponding somite in two or more worms does not always have the same number of chætæ.

the chætæ swell up to nearly twice their real diameter, so that this method alone would give a wrong impression as to their real shape; the terminal parts appear to be harder, and are not so affected.

Table of Arrangement of Chætæ.

	Dorsal Bundles.		Ventral Bundles.	
Segment.	Right.	Left.	Right.	Left.
II.	2 or 3	2 or 3	3 or 4	3 or 4
III.	4 (+ 1)	4 (+ 1)	3 (+ 2)	3 (+ 1)
IV.	4 (+ 1)	4 (+ 1)	3 (+ 2)	4 (+ 1)
V.	6 or 7 (+ 2 or 3)	6 (+ 2 or 3)	3 (+ 1)	4 (+ 1)
VI.	7 (+ 3)	8 (+ 3)	3 (+ 1)	3 (+ 1)
VII.	7 (+ 3)	10 (+ 1)	3 (+ 1)	3 (+ 1)
VIII.	9 (+ 3)	11 (+ 3)	3 (+ 1)	3 (+ 1)
IX.	11 (+ 2)	11 (+ 1)	3 (+ 1)	3 (+ 1)
X.	9 (+ 1)	9 (+ 3)	2	2
XI.	6 (+ 1)	5 (+ 2)	2 (or 1)	2
XII.	6 (+ 3)	6 (+ 2)	2 (+ 1)	1 (+ 1)
XIII.	4 (+ 2)	6 (+ 1)	1 (+ 1)	1 (+ 1)
XIV.	3	3	1 (+ 1)	1 (+ 1)
XV.	2 or 3	2 or 3	2	2
XVI.	2	2	2	2
XVII.	2	2	2	1 or 2
XVIII.	2	2	2	2
XIX to XXIV.	2	2	2	2
XXV to end.	2	2	1	1

Note.—The strong figures represent the palmate chætæ; the (+ *x*) represents young chætæ, which do not protrude.

But I have found, not unfrequently, examples which show a slight difference in the position of the palmate bundles.

In two or three specimens the chætæ of Segment xiv were palmate, like those of xiii.

In another specimen the dorsal bundle of one side of Segment xiv consisted of four palmate and one furcate chætæ, that of the other side only of furcate chætæ.

In another a similar asymmetry of Segment xv occurred; i. e. on one side the bundle consisted of one furcate and two palmate chætæ, those of Segment xiv being all palmate.

Still further, in one specimen, whilst the chætæ of the dorsal bundles of Segment XIII were as usual palmate, those of Segment XII were furcate.

Seeing that in Psammoryctes and in Tubifex we get certain chætæ which are neither simple crotchets nor completely palmate (see Vejdovsky's figs. 11 and 4, pl. viii), I looked carefully for similar intermediate forms in Heterochæta, and for a long time I looked in vain, but ultimately I was successful in finding somewhat similar "intermediate" or "multidentate" chætæ. The one figured (fig. 15) was from one of the dorsal bundles of Segment XIV of one specimen; it occurred with three typical palmate forms, and there were no crotchets. Curiously enough it was not at the side of a bundle, but between the 2nd and 3rd palmate chætæ. These "intermediate" chætæ have one or two teeth between the prongs.

One specimen I noted, and here represent (fig. 16), in which a great amount of divergence from the typical arrangement was accompanied by intermediate conditions of the chætæ. This may be tabulated thus:

Abnormal Specimen.

Segment.	Right Dorsal Bundle.	Left Dorsal Bundle.
II.	3 furcates	3 furcates.
III.	1 furcate (most dorsal of bundle) 2 intermediates	3 furcates.
IV.	1 furcate (dorsal) 3 intermediates	2 furcates. 1 large palmate. 2 small palmates.
V.	5 (+ 1) palmates . . .	5 (+ 1) palmates.

VI to XIII (inclusive) were normal.

Dorsal Chætæ.

Segment.	Right.
XIV.	3 palmates.
XV.	1 furcate and 1 intermediate.
XVI.	1 palmate and 1 furcate.
XVII, &c.	2 furcates.

The palmate chætæ are usually considered as special modi-

fications of the furcate or crotchet-shaped chætæ, with the multidentate forms as an intermediate condition.

I am inclined to regard them in a different light, for—

(*a*) If a palmate bristle be viewed from its edge, I have shown that the tips of the teeth are all curved, and this curve resembles the curve of a furcate chæta if the lower tooth were removed.

(*b*) The divergence of the two outer teeth or ridges of the comb is different from that of the prongs of the fork, in which both prongs are directed towards the same side of the stalk, and the tip of each is frequently curved downwards in the same direction. In the palmate bristles it will be seen that neither of these things occurs (see also Pl. VII, figs. 33, *a*, *b*, 36, *c*, *d*).

(*c*) The plane of the head, i. e. the two prongs of the furcate chæta, is in a state of rest parallel with the long axis of the body, whereas that of the palmate bristle is at right angles to the axis of the body.

(*d*) The so-called "intermediate" forms, or "multidentate" forks, do not represent a stage in the formation of the ctenate bristles. The two prongs are similar to those of the simple furcate forms in relative size, curvature, divergence, &c.

(*e*) I would rather regard the ctenate chæta as having been derived from a simple "sigmoid" chæta (such as is common amongst earthworms, some Lumbriculidæ, some Enchytræidæ, and in Phreoryctes) by a flattening and expansion of the dorsal extremity, so as to form the "membrane," which then becomes thickened or ribbed to give rise to the palm-leaf-shaped arrangement; whilst the furcate chætæ, which are so common amongst the Oligochæta generally, may have been derived similarly from the "sigmoid" form by the appearance of a notch at the extremity, which became deepened to form the angle between the two prongs, these in their turn becoming more and more developed, the plane of two prongs being at right angles—with respect to the axis of the original chæta—to the plane of the "membrane" of the palmate forms.

The "multidentate" chætæ will then be a further develop-

ment of the fork, but not in the direction of the palmate type.

The sigmoid form itself is not necessarily the primitive form of chæta ; it is possible that a straight spine, such as we find in the Enchytræids, is an earlier form, which may have given rise to the capilliform shape by elongation, and to the sigmoid form by curvature, and hence to these other forms.

Amongst other external features which are of interest may be mentioned the distinct annulation of the anterior segments of the body (fig. 3). This is distinctly visible during life, and can be detected in longitudinal sections. Each segment is marked out by three grooves into four rings, of which the third is the largest, and on this the chætæ are embedded. The most anterior segments show only two of these grooves, and on the clitellum they are present only ventrally. This feature is mentioned by Claparède, and is of more frequent occurence in aquatic Oligochæta, as in earthworms, than is usually supposed.[1] It is indistinctly marked in some Naids. Claparède mentions the fact in Tubifex and Limnodrilus. It is present, in fact, in the majority of this family, and is carried to an extreme in Branchiobdella. It is present in Hemitubifex, though rendered less noticeable and even almost obscured by the dark cuticular papillæ. In Heterochæta, however, it is so distinct that it is almost the readiest means of distinguishing, under a low power, this worm from other forms with which it occurs, for the characteristic chætæ are not visible if the animal presents its ventral surface upwards.

I am unable to say what may be the "Langsfürchen" in the skin, mentioned by Claparède. I see no such grooves. His figure may represent the bundles of longitudinal muscles which can be seen during movement of the worm, and will at times be thrown into wavy lines such as his drawing represents.

The shape of the prostomium is exhibited in my figs. 3

[1] For example, Mr. W. Hatchett Jackson, in the 2nd edition of 'Forms of Animal Life,' states on p. 593 that "annulation of the somites is very rare."

and 16. It is conical in its general outline, with a circular groove near the tip, giving it a pointed appearance.

The male pores (spermiducal pores) are, as is always the case in the Tubificidæ, in Somite XI slightly dorsal of the ventral chætæ.

The spermathecal pores are in a similar position in Somite X. In both cases the cuticle dips inwards at the pore, and is folded around its lip.

The vascular system is of the usual Tubificid[1] type. There is a pair of lateral dilated hearts in Somite VIII. These contract not together, but alternately. In the genital segments these vessels are contractile, and lie on the sperm- and ovi-sacs; in other segments a pair of narrow convoluted vessels lie immediately below the body-wall.

The most important system of organs after the chætæ are, of course, the genitals. These are shown in situ in fig. 17, which is taken from a careful sketch made from the living worm, sufficiently compressed to prevent movement, and to allow the organs to be seen without undue distortion or displacement. The clitellum covers the dorsal surface of XI, XII, and part of X as far as the chætæ, sometimes even part of XIII.

The Male Organs.—A pair of testes in the 10th segment are attached to the anterior septum of this segment.

The funnels of the sperm-ducts lie against the posterior septum of the 10th segment; from the funnel on each side the narrow ciliated duct passes, with only slight undulations, back through the Segment XI and into Segment XII. Here it enters the glandular "atrium;" this narrows, loses its glandular coat, passes forwards into Segment XI, and here opens to the exterior.

The "cement gland," or prostate, lies in Somite XII, and here opens into the atrium.

[1] In a recent paper ("Monog. českých Tubificidů") Stolc gives some excellent figures of the arrangement of vessels in several genera, and represents several new points; e. g. the lateral hearts in his two new genera Lophochæta and Bothrioneuron arise, not from the dorsal, but from a supra-intestinal trunk.

The male apparatus is represented in greater detail in fig. 18, as seen when "squeezed" out of the body, with exception of the funnel, which remained inside.

The funnel, as in all the aquatic Oligochætes, is simple, and not folded as in earthworms. In the Tubificidæ it is a very large, flattened, and shallow structure, as is also the case in the Lumbriculidæ and Phreoryctidæ. In the Enchytræidæ it has a characteristic form, being long, narrow, thick-walled, and projecting far into the cavity of its segment.

In Heterochæta the funnel, though usually lying flat against the face of the septum, undergoes, with the contraction and extension of the worm, a corresponding movement, in that the lips move to and from the septum, so that its other extreme position is represented in fig. 19.

The duct does not leave the funnel in the centre of the latter, but slightly to its outer side. This asymmetrical condition is shown by Beddard in Clitellio arenarius; but in all other figures by Claparède, Vejdovsky, &c., the duct is represented as leaving the funnel in its centre. Whether there is any differential character in this feature I do not know. I rather think that this is not the case, but that the drawings are to some extent diagrammatic, and make no pretence to represent the thing accurately.

The sperm-duct is thin-walled and ciliated internally, as is always the case.

The "atrium" (fig. 18) is divisible into two regions here, as in Psammoryctes—a region coated with granular cells, which give to it a dark appearance (*gl. atr.*); and a thin-walled, narrower region (*n. gl. atr.*), which passes to the penis.[1]

There are no cilia in the "atrium," using the word to include all that part of the apparatus after the entrance of the solid "prostate." The terminal part of the atrium passes into

[1] To this dark granular region Vejdovsky, in his description of Psammoryctes, gives the name "seminal vesicle," whilst the long narrower region between it and the penis is termed by him the "cement duct."

the protrusible penis, which is surrounded by a specially thickened chitinous coat. The figures 18, 21, 22, representing the arrangement of this region of the duct, aid the description. It will be seen that the male pore leads into a chamber (penial chamber, *a*, *b*) lined by cuticle invaginated at the male pore. Projecting from the bottom of this penial chamber (or "cloaca" of Claparède, or "ductus ejaculatorius" of Vejdovsky) is the "penis." This consists of a soft central part, the "glans," and a thick, refracting, chitinous coat (Vejdovsky's "penis tube"), which has a characteristic form. It is nearly cylindrical, the edge of the outer end of the cylinder being bent outwards so as to form a rim, and is much more noticeable than that of Psammoryctes, Spirosperma, &c. (cf. this with the penis of other members of the family).

The internal soft part is perforated nearly axially by the narrowed continuation of the atrium, the external aperture of this duct being excentrically placed on a protuberant "glans penis" (of Vejdovsky). I have not seen this penial apparatus in a protruded condition, but no doubt a similar process occurs here as in Tubifex.

When I first examined the genital duct, separated from the animal, I found that the "cement duct" (of Vejdovsky) and the "seminal vesicle" exhibited irregular dilatations, as seen in fig. 20, *a* and *b*. I therefore isolated some eight or nine ducts, in order to ascertain whether these dilatations were constant, and I soon found that such was not the case—that these swellings are only artificially produced. This was confirmed by the fact that in situ there are not such definite swellings.

In the fully mature worm Segments IX to XIV, or even XV, are occupied by developing ova and spermatozoa. In some cases, such as the one figured, we find both genital cells fairly equally developed; whereas in other specimens the spermatozoa are predominant, and no large ova are present, and vice versâ.

The developing spermatozoa are included in definite sacs, the sperm-sacs, which are provided with thin membranous

walls, upon which are greatly convoluted and contractile commissural blood-vessels.

These sperm-sacs are asymmetrically arranged. There is usually one in Segment IX, and another starting in Segment XI, and extending back as far as Segment XIV or XV, pushing the intervening septa in front of it. Very usually, though I believe not invariably, this sac crosses from one side of the body to the other dorsally of the gut.

Besides these two sacs (Claparède's "testicles") masses of developing spermatozoa more or less fill Segment X. The minute structure of various parts of the male apparatus deserves a brief description, not from any peculiarity special to the genus, but because we have but few details of the histology of these aquatic Oligochætes. The figures of Claparède, Vejdosky, Eisen, &c., are, in the main, somewhat diagrammatic, even where these authors intend to show detailed structure. Beddard has recently contributed some facts as to the minute structure of Hemitubifex and Phreoryctes, and Michaelsen has recorded something of the histology of Enchytræids.

The sperm-duct, when its surface is viewed, is seen to be striated transversely, as is the case in Tubifex, &c. The minute structure, as seen in sections, is exhibited in my fig. 23, which includes a transverse and a longitudinal section of the sperm-duct.

In transverse section there is a remarkable "striation" of the wall, which is apparently due to radial arrangement of the granules in the cells; this is seen even better in a series stained in hæmatoxylin than in the borax-carmine sections drawn. I can see no boundaries to the cells; and the nuclei are not elongated radially, but tangentially: they are, in fact, ovoid in shape, the long axis being at right angles to the axis of duct, so that in longitudinal section the nuclei have circular outlines. I have seen a similar arrangement in Tubifex, both as regards striation and nuclei.

In earthworms, e.g. Lumbricus, Perichæta, the striation is present, but the nuclei appear to be spherical, giving a

circular section in all directions. Beddard,[1] in his figure of the sperm-duct of Hemitubifex, shows a different arrangement.

The two parts of the atrium, already distinguished externally, are equally distinct in histological structure: the non-glandular part (fig. 23, *ngl. atr.*) is lined by flat cells, with horizontally elongated nuclei and granular protoplasm; whilst the glandular region (*gl. atr.*) is lined by cells of a totally different shape. The epithelium here is more or less cubical; the cells are glandular—at any rate vacuolated, as if a secretion had been discharged; the protoplasm, with darkly staining granules of comparatively large size, is chiefly found in the outer part of the cell, where, too, is the round nucleus (fig. 25); the spaces, or vacuoles, appear sometimes to be occupied by an extremely fine substance—so fine that it is impossible to detect whether it is homogeneous or finely granulated, and requires an apochromatic to be seen at all.

The prostate is a solid structure, built up of a mass of cells having essentially the same structure as the preceding, though differing in shape (fig. 24). These cells are pyriform; the granules are larger and distinctly spherical; probably the neck of each cell serves as a duct, and pours the secretion into the atrium independently of its neighbours.

Mr. Beddard's[2] drawing differs slightly from mine, chiefly as to details, which is perhaps due to the method of preservation. If the cells in Heterochæta were a little emptier, we should have an appearance something similar to that shown by him for Hemitubifex.

I may say that the isolated cells here figured are drawn from sections, and not from teased preparations.

The prostate, like the sperm-duct and atrium, is surrounded by a delicate membrane (*c. ep.*), with a few scattered nuclei; this membrane is continuous, and is the cœlomic epithelium. The atrium has in addition a muscular coat, as shown in the figure (*mus.*).

[1] "On Certain Points in the Structure of Clitellio," 'Proc. Zool. Soc.,' 1889, p. 485, pl. xxiii, fig. 5.

[2] Loc. cit., fig. 7.

In fig. 22 I have drawn a section along the penis, in order to show the character of the cells which give rise to the chitinous penial sheath, and their continuity with neighbouring epithelia. The figure is sufficiently explained, and confirms the drawing (fig. 21) which is made from a living specimen, but where of course only the cuticular structures (except the penis itself) are shown.

The Female Organs.—There is a pair of ovaries in Segment XI, usually concealed in a fully developed individual by other structures.

As is the case in other Oligochæta, eggs leave the ovary and undergo further development in an "ovisac;" this in Heterochæta occupies Segments XIII, XIV, and sometimes XV. Usually this sac contains two or three very large ova, one in each segment; there is a contractile vessel in the wall of the ovisac, as in the case of sperm-sacs.

The oviduct is a small funnel opening externally between XI/XII.

As in other members of the family, there is a pair of spermathecæ in Segment X. Each spermatheca consists of a short, narrow duct, and an elongated, wide, tubular sac. The duct is shorter and the sac longer than in most other genera, the duct being about the same size as in Limnodrilus Udekemianus, Claparède. The pore lies in a line with the spermiducal pore, and, like it, has the cuticle invaginated around it.

The sac of the spermatheca may be entirely confined to Somite X, or may extend into the neighbouring segment. In the specimen from which the figure is taken the spermatheca of the right side is wholly in Segment X; that of the left side had pushed its way into the succeeding somite. In other specimens I have seen the sac of one side extending into Somite IX, that of the other into Somite XI.

The spermatheca, though not externally divisible into very marked regions beyond duct and sac, shows internally certain peculiar cells near the pore (cf. Vejdovsky's picture of Tubifex, Pl. IX, fig. 17). The greater part of the sper-

matheca is lined by columnar cells (fig. 26), the nuclei of which are usually situated near the outer margin. These cells are very granular, and their internal margin sometimes indistinct. But near the neck the cells are pyriform (fig. 27), as in Vejdovsky's figures; and these cells are extremely finely granulated, the nucleus being in the dilated part of the cell, which projects into the cavity of the spermatheca, so that in this region the inner limit of the epithelium is quite irregular.

The spermathecæ are filled with the characteristic Tubificid sperm-ropes (I prefer this term to spermatophores), of which I counted in one specimen as many as thirty-five; some of which were completely formed, others incompletely. A completely formed "rope" is shown in fig. 28, its structure in figs. 29—31.

It is spindle-shaped; one end being drawn out into a point, the opposite end being truncated, slightly knobbed, and apparently perforated. The wall is highly refracting and forms a fairly thick coat, in which the heads of the spermatozoa are embedded (*a*); immediately below this is, in optical section, a layer of granules (*b*) (? sections of spermatozoa), and the interior is filled with loose spermatozoa in addition to those embedded in the wall, whose freely projecting tails give rise to the movement of the whole apparatus. When partially crushed, bundles of spermatozoa protrude from the interior through any breaks in the wall (fig. 30).

Though spindle-shaped like the sperm-rope of Psammoryctes or Limnodrilus, it lacks the peculiar "spines" on the neck which occur in the former, and is relatively much longer, narrower, and more pointed than in the latter.

The structure of spermatophore is further illustrated by fig. 31, which is drawn from a section through a spermatheca. The homogeneous layer (*a*) is in these preserved specimens very highly refractive and scarcely stained. By the use of an apochromatic, and regulation of the light, the heads of the spermatozoa could just be detected; the lines representing them in the figure are much too coarse.

I have added a figure of a specimen of the worm after sexual

maturity is over (Pl. VI, fig. 32), as it shows very distinctly the shrunken sperm-sacs, the ovaries and testes. The spermathecæ are apparently undergoing degeneration ; they are filled with highly refracting globules. No trace of the sperm-duct or atrium, nor even penis was present; but in other specimens traces of the male apparatus could be detected. This disappearance of the penis appears to me particularly remarkable, though I am unable to say whether it is due to its solution or absorption by the cells, or whether the hard coat is thrown off.

Comparison of Heterochæta with other Tubificidæ.

The nearest genus to Heterochæta is undoubtedly Psammoryctes (Pl. VII, fig. 33), on which alone are found palmate chætæ closely resembling those of the former genus. In its generative apparatus, too, there is a pretty close agreement,[1] in the division of the atrium into two regions, and in the general form of the chitinous penial coat; but this is quite characteristic in Heterochæta. The chief differences between the two genera are (*a*) the restriction, in the latter genus, of the palmate chætæ to Segments v to xiii, which in Psammoryctes commence in Segment ii and extend to x; and (*b*) the absence of capilliform chætæ in Heterochæta. As the various genera of aquatic Oligochæta occur pretty abundantly in England, and as we have no brief summary of generic characters, I have brought together the chief characteristics in the form of a series of figures, and will point out here the leading features of these genera.[2]

Commencing with the chætæ of the dorsal bundles—for those of the ventral are essentially similar in all the family except Telmatodrilus, we have a fairly ready means of distinguishing groups of genera.

[1] I have not been able to see the dilatations in the atrial duct described by Vejdovsky.

[2] Stolc, in a recent paper in the Czech language, adds considerably to our knowledge, so far as I can judge from the plates.

Telmatodrilus, Eisen, possesses only one kind of chæta, simple, unforked, sigmoid forms, resmbling those of Enchytræus.

Limnodrilus and Clitellio likewise possess only one kind of chætæ (Pl. VII, fig. 35), namely, the furcate or "crotchet," which may vary in detail in different regions of the body.[1] In Hemitubifex, too, there is only one kind generally, though Eisen and Beddard mention capilliform chætæ as "sometimes" occurring. I have not seen them in H. ater. Tubifex (fig. 34) and Ilyodrilus (fig. 33) present us with capilliform chætæ, either only anteriorly in Segments III to X (or thereabouts) in the former, or throughout the body in the latter genus; these chætæ are confined to the dorsal bundles, and with them occur furcate chætæ, which possess very usually two or more accessory prongs between the two main prongs in Tubifex,[2] or a membrane, without ridges or teeth, in Ilyodrilus. In both genera these modified furcate chætæ occur in anterior segments only.

Further, in Spirosperma (fig. 36) capilliform chætæ occur all along the body, and are accompanied throughout by a peculiar variety of palmate chætæ (see further on in this paper), which are small and inconspicuous.[3] They differ in shape and size from those of Heterochæta and Psammoryctes.

Another set of characteristic modifications affects the male apparatus.

The shape of the atrium, presence or absence of prostate, and penial coat are among these. The prostate is absent in Clitellio and Ilyodrilus. In the remainder it is a somewhat kidney-shaped, solid mass of cells communicating with the atrium at the point of entrance of sperm-duct.

[1] Bothrioneuron, Stolc, so far as chætæ are concerned, agrees with Limnodrilus.

[2] I have not seen the membrane between the forks, as figured by Professor Lankester.

[3] In Stolc's genus Lophochæta somewhat similar chætæ occur in the dorsal bundles, together with peculiar feathered capilliform chætæ; but the exact distribution of these I am unable to give, as I have not yet had Stolc's paper translated.

In Telmatodrilus there are eight or more small isolated prostates.

The atrium is relatively short in Tubifex and Ilyodrilus,[1] where it is glandular throughout, and there is no distinction of a non-glandular portion or atrial duct.

In Limnodrilus there is a short non-glandular region, which is larger in Spirosperma.

In Psammoryctes (see below) and Heterochæta[2] the glandular region is relatively small, and the non-glandular portions greatly extended.

I append figures of the chitinous coat or tube of the penis (Pl. VII, fig. 37), by which I understand a thick, refracting modification of the cuticle, such that it can be readily recognised.

Such a penial tube is absent in Tubifex and Ilyodrilus.[3] It is short and nearly cylindrical in Spirosperma (37, *c*), Psammoryctes (37, *c*), and Heterochæta (Pl. VI, fig. 21). The last, however, has the outer edge turned out so as to form a rim.

In Telmatodrilus (37, *b*) and Hemitubifex[4] (fig. 37, *a*) it is a short truncated cone (I cannot find a description or figure of this part in Clitellio).

In Limnodrilus (including therein Camptodrilus, Eisen) the tube is usually very long and relatively narrow, cylindrical, or constricted near the middle, or trumpet-shaped (figs. *d*, *e*, *f*). In L. Hoffmeisteri it has a peculiar free end (37, *g*), and in L. silvani it is flask-shaped (fig. 37, *h*).

[1] Stolc figures the male apparatus of Ilyodrilus: the atrium appears spherical, and is surrounded by a layer of large cells, which Beddard would call the "prostate," resembling that of Stylaria, &c.

[2] Lophochæta resembles these two genera. Bothrioneuron presents several peculiarities in the male apparatus.

[3] As also in Bothrioneuron.

[4] In Lophochæta also.

Spirosperma ferox, Eisen.[1]

This worm has hitherto been found only in Sweden, and has been observed by Eisen alone.[2]

I have found specimens in the Thames and in the Cherwell.

It is readily recognised by the naked eye, owing to its grey colour, with a bright white clitellum occupying Segment XI, and extending into X and XII. The grey is sometimes less marked, apparently in immature specimens, which are greyish red. The grey colour is due to numerous closely set papillæ, of rather irregular form, usually irregularly rectangular, with long axis, as Eisen states, at right angles to the worm's length; but they are not "dark," as he says. They look dark by transmitted light, but if the surface is viewed by direct reflected light they are white, the dark colour being due to the feebly yellow globules in the papillæ.

The worm is six eighths of an inch long, and relatively thick anteriorly. The chief anatomical point is that the chætæ of the dorsal bundles throughout the body are capilliform, accompanied by, in most cases, extremely delicate webbed chætæ. These are rather stouter in the first half-dozen segments than posteriorly, but throughout they are less than half the thickness of the capilliforms (fig. 36, *c*, *d*).

The shape of these "webbed" chætæ is quite distinct from the multidentate, or even the webbed chætæ of Tubifex, or the palmate chætæ of Psammoryctes and Heterochæta, though they approach the latter.

The ventral chætæ are not all alike (fig. 36, *e*, *f*); they are all crotchets, but in the first six bundles the proximal prong is shorter than the distal prong (*f*). Behind the reverse is the case, and the proximal prong is extremely stout and strongly recurved (*e*), somewhat as in Psammoryctes, but more so.

The capilliform chætæ are usually four per bundle up to

[1] "Oligochætological Researches," 'Annual Report of the Commissioner of Fish and Fisheries for 1883," Washington, 1885.

[2] Stolc has found it in Bohemia.

Segment x, behind which there are three per bundle. In Segments v and vi I noticed six per bundle.

The webbed chætæ are usually two, rarely three per bundle.

The length of the latter is $\frac{8}{1000}$ mm., and of the capilliform chætæ $\frac{32}{1000}$ mm., though those of the Segments vi, vii, viii are $\frac{40}{1000}$ mm.

I have little to add to Eisen's description and figures. The body-wall is so opaque that it is difficult to see accurately the contained organs. By compressing the worm I released the genitals, which agreed almost exactly with Eisen's figures, except that the sperm-rope, of which I found only one in each spermatheca, is much less, and less regularly, coiled than he represents.

Note on Psammoryctes.

It is worth recording that a species which I, for the time, regard as Ps. barbatus, Vejd. (Tubifex umbellifer, Lankester), occurs in the Cherwell, in the mud amongst the roots of reeds. As far as I am aware it has not been recorded from a British locality since Professor Lankester[1] found it at Barking in brackish water.

The palmate chætæ (fig. 33, *a*), are rather different from those of Heterochæta, in that the "head" makes a slight angle with the "stalk," a fact which is not represented in Vejdovsky's nor in Lankester's drawings. It may, perhaps, be characteristic of a new species.

The ridges on the membrane are usually twelve or thirteen in number, and the head has the same curvature (fig. 33, *b*) as in Heterochæta. In existing drawings of these chætæ the outermost prongs are represented as stronger than the rest. This is not the case in my specimens. It is a matter of focussing, as in Heterochæta.

I figure also the ventral chætæ from different regions of the body. Those of the posterior segments (fig. 33, *e*) have a slightly different curve from that represented in existing figures. These, too, may turn out to be specific differences. But I will wait

[1] 'Annals and Mag. Nat. Hist.,' 4th ser., vol. vii, 1871.

till I obtain other specimens from Barking before giving a new name on these grounds.

I find no chætæ, either dorsally or ventrally, in Segment xi in mature worms.

In Segment x the ordinary ventral chætæ are replaced in mature forms by a single long rod-shaped chæta on each side, immediately in front of the pore of the spermatheca.[1]

I do not find the "dilatations" which Vejdovsky figures on the sperm-duct between atrium and penis so long as the duct is uninjured; when, however, it is separated from the body of the worm by pressure there is a variable number of dilatations, as in Heterochæta.

Note on Chætæ of Tubifex rivulorum.

Professor Lankester[2] was the first to record the existence of secondary prongs or teeth in the fork of the dorsal chætæ of this worm, and mentions a web passing between the two main prongs. I have not been able to detect this web, but have not had a very large series of specimens under observation for this purpose. I treated the chætæ in the usual way, i. e. I dissolved the worm, on a slide, in KHO, mounted the chætæ in glycerine, and examined them with a Zeiss's homogeneous immersion lens, but I was quite unsuccessful. It is not impossible that the specimens which Lankester examined belonged to Eisen's genus Ilyodrilus, in which such a membrane exists. But I have noted some peculiar modifications of these dorsal chætæ, which I figure in Pl. VII, fig. 34, *a*, *b*, *c*, *d*; one of the most curious of which is the occurrence in more than one case of a tooth outside the chief prong.

Stylodrilus Vejdovskyi, n. sp.

In a gathering made on July 17, just below Goring-on-Thames, I found a few small red worms about one third the

[1] Since writing this paper I have seen Dr. Antonin Stolc's memoir on Bohemian Tubificidæ, in which he figures this chæta, which is grooved distally, and is inserted in a sac into which a pair of glands open, close to the pore of the spermatheca.

[2] Loc. cit.

size of an ordinary Tubifex—namely, about an inch in length. I found these worms amongst the roots of the bur-reed, which I was examining for Criodrilus, and with them I found a specimen of Spirosperma. Hitherto only two species of Stylodrilus have been described: the first by Claparède,[1] St. heringianus; and the more recent species by Vejdovsky,[2] St. gabretæ. The differences—and these appear to me slight—between the two are such that had not Vejdovsky examined both species, one would be inclined to regard these differences as merely ones of observation. The specific characters of St. Vejdovskyi are as follows:

Prostomium conical, two and a half times as long as the buccal segment, and differing in shape from both that of the previous species (Pl. VII, fig. 42).

The segments, after the first three, are biannulated, the smaller annulus being anterior, as in St. heringianus. This annulus is very small in anterior segments, but behind the clitellum it is a third as large as the posterior annulus (Pl. VII, fig. 43).

The chætæ are essentially all alike; in the other two species some of the ventral ones are simple sigmoid, unnotched chætæ. In St. heringianus these are irregularly arranged, whilst in St. gabretæ they occur only in the pre-genital bundles. But in the present species, though with a low power some chætæ appear sigmoid, a high power reveals an indication of the notch; and the young, non-protruded chætæ are notched as markedly as in the dorsal and posterior ventral chætæ (fig. 44). In fact, these anterior ventral chætæ appear to have had the small upper tooth worn away.

In St. Vejdovskyi, then, all the chætæ are notched; and, like those of Lumbriculus, have the distal or upper tooth much smaller than the lower.

The dorsal vessel is not dilated in any segment; while in St. gabretæ there are dilatations in Segments VI and VII.

[1] Claparède, "Recherches sur les Oligochétes," 'Mém. Soc. Phys. et Hist. Nat. Genève,' xvi.

[2] 'System und Morph. d. Oligochaeten.'

The sperm-sacs are paired, and have the normal arrangement extending as far back as Segment XVI; there are three large eggs in XV, XVI, and XVII respectively (in one specimen one egg occupied the 16th and 17th segments).

The spermatheca lies in Segment IX entirely; in St. gabretæ it extends also into the next segment. I found no crystals, such as Claparède found, in the spermatheca of St. heringianus.

The characteristic penis differs from that of both the previous species in shape and size. In St. Vejdovskyi it has a length just a little greater than half the width of the body (fig. 43). It is not so narrow relatively as that of St. gabretæ; it is not so pointed as in St. heringianus. In normal position its free end is on a level with the chætæ of Segment XI.

The nephridia have a very peculiar arrangement. The first nephridial funnel lies in Segment VI, just in front of the posterior septum; the tube passes backwards with only slight undulations and coils as far as the middle of Segment X, and then returns alongside itself into Segment VII, where it opens externally in front of the ventral chætæ.

The second nephridial funnel lies in normal position in Segment XII; its external pore is in XIII, and the looped tube passes backwards as far as the hinder part of Segment XV.

The third funnel is in Segment XV, the nephridiopore in XVI, and the loop lies wholly in this segment. This is the normal condition for the following nephridia; but I observed one case in which the tube passed through two segments.

This condition of the nephridium is very similar to that described by Vejdovsky for Phreatothrix, and is unknown elsewhere amongst the Oligochæta. The structure of the nephridium agrees with Claparède's figures and description, although in that species he states (p. 265) that the first nephridium lies in Segment VII; that there are none in VIII, IX, X, XI, or XII, and that they reappear in XIII.

The length of St. Vejdovskyi is about an inch; none of my specimens exceeded this length. In colour they are bright red, with a tendency to orange; but the colour is much less

marked anteriorly and posteriorly, where it is dull pale yellow. They are very active little worms. I have found them not only in the Thames, but in the Cherwell, just above Oxford.

Nais elinguis, O. F. Müller.

In a gathering from a ditch in the immediate neighbourhood of Oxford I found, together with a number of specimens of Chætogaster diastrophus, Gruithuisen, some Naids showing zones of budding. A glance at the dorsal chætæ of these latter determined the species as N. elinguis.

It may be useful to recall the characteristic chætæ of this species. In addition to the long capilliform chætæ of the dorsal bundles (fig. 38, *a*), which commence on the 6th segment, there are short needle-like forms, and a third kind, a straight spear-like chæta notched at the free end, with a swelling or node on the stalk at about one third or one fourth from the free end. There are usually two capilliform, two or three short needles, and two notched spears. The ventral chætæ present no important characters (fig. 38, *b*). The blood is red, as in Paranais littoralis and other species.

These specimens were gathered on May 10th of this year (1891), and were then actively reproducing asexually. They were, after examination, placed in a greenhouse; and on the 26th of May, when I examined them again, most of them were sexually mature, whilst some were still showing zones of budding.

In these asexual forms I find generally that $n = 13$, according to Professor Bourne's use of the letter;[1] but one case I noted in which $n = 15$.

The sexual worms agree, in respect of the position of the organs, with Stylaria: that is to say, there is a pair of testes in Somite v, in which also are situated the spermathecæ; a pair of ovaries in Somite vi, in which are also placed the atria and their apertures.

The sperm-sacs have the arrangement shown in fig. 39;

[1] "Notes on Naidiform Oligochæta," this Journal, vol. xxxii, p. 335.

namely, a pair in Somite VI, and a long unpaired, asymmetrically placed sac extending through Segments VII, VIII, IX, and into X.

Masses of developing ova were observed in Somites VII, IX, XI, and a large ovum in Segment X.

I have thought it worth while to figure the arrangement, as Dr. Bourne gives a different position for the "testes" and "ovaries" for Paranais littoralis, which I was unfortunately unable to find in a mature condition. He figures a large, asymmetrically placed mass occupying Segments VIII and IX, which he speaks of as "testes," and he indicates as "ovary" a single mass of developing ova in Segment X. Now, this would be a very exceptional position for the gonads in the family Naididæ; and the "testis" of Oligochæta is not a large structure, but a small organ, occupying only a part of one segment. I cannot help thinking that Bourne has made a slip in writing of these structures as the gonads; he meant probably to speak of them as the sperm-sacs and ovisacs respectively.

It is a well-known fact that in the sexually mature Naid genital chætæ replace the ventral bundles in Segment VI, and that the dorsal chætæ, like the ventral ones, drop out, but are not replaced (fig. 40).

I figure a portion of a nearly mature worm, i. e. with sexual organs, in which the dorsal chætæ are still in situ. The ventral chætæ of one side are also present, but on the other side have been replaced by the genital chætæ (fig. 41). These are stouter and longer than the ordinary ventral chætæ, and are not forked (fig. 38, *c*).

The Supposed Constancy of *n* in a given Species of Naid.

In a recent contribution ('Quart. Journ. Micr. Sci.,' xxxii, Part 2, June) on the Naididæ, Professor A. G. Bourne adds many facts to our knowledge of the family, and gives the position of the zone of budding for many of the species, but says nothing about it for N. elinguis. He regards the position of the zone of budding as a constant character for

the various species, and designates this position by *n*, which signifies the number of segments in front of the zone.

Now, from my recent observations on this phenomenon, some of which were made before the publication of Professor Bourne's paper,[1] I believe that he is rather too dogmatic on this point; for he only mentions one exception, and that for Pristina breviseta, A. G. B., whereas I have found considerable divergences in the value of *n* from the value given by him. For example, a number of Stylaria lacustris, collected in different places and at different times, were examined from this point of view.

Dr. Bourne gives for this species "$n = 27$." I find, however, as will be seen from the following table, a good deal of variation in the position of the zone. The list refers to two sets of specimens, each individual being indicated by a letter.

A . . .	$n = 20$	F . . .	$n = 30$
B . . .	$n = 27$	G . . .	$n = 24$
C . . .	$n = 24$	H . . .	$n = 24$
D . . .	$n = 30$	J . . .	$n = 25$
E . . .	$n = 24$		

Six specimens were without zones.

In another lot—

K . . .	$n = 27$	N . . .	$n = 25$
L . . .	$n = 27$	O . . .	$n = 34$
M . . .	$n = 30$		

Three specimens showed no zone.

In all these cases I am counting as Professor Bourne counts; namely, the 1st setigerous segment is Segment II, so that the first dorsal bundle occurs in Segment VI.

Again, in Nais barbata he states, on p. 344, "$n = 17$." I examined a limited number of these, and found the number by no means restricted to 17. I have unfortunately mislaid my notes on the point, but four specimens, taken at random before I had seen his paper, were stained and mounted. Of these two have $n = 14$, and in the two others $n = 15$.

[1] Professor Lankester kindly allowed me to see a proof of the paper, and my attention was thereby drawn more particularly to some of these points.

Illustrating Dr. W. Blaxland Benham's "Notes on some Aquatic Oligochæta."

Heterochæta costata.

Fig. 1.—The worm of the natural size.

Fig. 2.—A specimen coiled, about twice natural size.

Fig. 3.—Side view of worm, enlarged, showing the characteristic arrangement of chætæ. The segments are numbered and the annulations shown. *Pr.* Prostomium. *Dors.* Dorsal bundles. *Vent.* Ventral bundles. *Cten.* Palmate chætæ.

Fig. 4.—One of the characteristic palmate chætæ from in front.

Fig. 5.—The "head" of a palmate chæta, more enlarged and in a different focus, showing now the apparently stronger outer prongs.

Fig. 6.—A palmate chæta from the side, to show curvature of head.

Fig. 7.—View of the free edge of a palmate chæta, showing curve, membrane, and ridges.

Fig. 8.—A palmate chæta seen obliquely from above, to suggest Claparède's possible mistake in describing these chætæ as "cup-shaped."

Fig. 9.—An abnormal palmate chæta, with ridges feebly marked.

Fig. 10.—A furcate chæta from the dorsal bundle of Segment III.

Fig. 11.—A chæta from a dorsal bundle behind Segment XV.

Fig. 12.—The free end of a furcate chæta from ventral bundle of Segment IV.

Fig. 13.—The free end of a chæta from a ventrai bundle of a more posterior segment to show the recurved proximal prong.

Fig. 14.—The "head" of a furcate chæta from in front, the transverse ridge being the lower or proximal prong.

Fig. 15.—An abnormal chæta, with two teeth between the chief prongs, from dorsal bundle of Segment XIV of a certain specimen.

Fig. 15*a*.—The dorsal bundle of Segment XIV, showing the abnormal multidentate chæta (which is drawn too large, relative to the normal ones).

Fig. 16.—Dorsal view of anterior end of a worm, showing abnormal arrangement of chætæ (see p. 194).

Fig. 17.—A few segments of the worm viewed ventrally by transparency

showing arrangement of organs. Drawn from a sketch of a living specimen slightly compressed. Portions of body-wall are represented showing the pores of sperm-ducts and spermathecæ.

Fig. 18.—The male duct isolated by compression. *Sp. f.* Spermiducal funnel. *Sept.* Septum between Segments x and xi. *Sp. d.* Sperm-duct. *gl. atr.* Glandular region of atrium. *n. gl. atr.* Non-glandular region of atrium. The extent of cilia is shown. The chitinous coat of the penis is represented in black outline.

Fig. 19.—A spermiducal funnel, with lips partly closed during movement of worm.

Fig. 20.—Two atria, isolated by compression, in order to show the artificial character of the dilatations of atrium. *sp. d.* Sperm-duct. *prost.* Prostate. *gl. at.* Glandular region of atrium. *n. gl. at.* Non-glandular region of atrium.

Fig. 21.—Enlarged view of penis from living worm, slightly compressed. The drawing is sufficiently explained. *a*, *b*, point to the circumpenial and pre-penial regions of penial chamber lined by invaginated cuticle. *v. ch.* Ventral chætæ.

Fig. 22.—Longitudinal section through penis, to show character of the cells of this region. *a.* Circumpenial; and *b*, pre-penial portions of penial chamber. *ch. pe.* Chitinous coat of penis, which is continuous with cuticle lining penial chamber. *ep. b.* Epidermis. *atr.* Portions of atrium.

Fig. 23.—Longitudinal section through portions of atrium and prostate. *c. ep.* Cœlomic epithelium covering prostate, sperm-duct, &c. *ep.* Epithelium lining the non-glandular part of atrium (*n. gl. atr.*). *ep'*. Epithelium lining the glandular part of atrium (*gl. atr.*). *mus.* Muscular coat of atrium. *pro.* Prostate. *sept.* Septum between Segments xi and xii. *sp. d.*, *sp. d'*. Transverse and longitudinal sections of sperm-duct.

Fig. 24.—A cell from prostate enlarged. *vac.* Vacuole.

Fig. 25.—A cell from epithelium of glandular part of atrium.

Fig. 26.—Section through spermathecal pore and neighbouring part of the the organ. *ep.* Epithelium of spermatheca (the internal boundaries of the cells have been made too definite). *ep'*. Epithelium of neck. *ep. b.* Epidermis. *c. ep.* Cœlomic epithelium. *mus.* Muscular coat. *p.* Spermathecal pore.

Fig. 27.—A cell from epithelium of neck of spermatheca.

Fig. 28.—A sperm-rope.

Fig. 29.—A portion of sperm-rope, more highly magnified. *a.* Very highly refracting wall, with heads of spermatozoa. *b.* Layer of granules within. *c.* Mass of spermatozoa in cavity. *d.* Tails of those spermatozoa whose heads are embedded in *a*.

Fig. 30.—Portions of crushed sperm-rope, the wall of which has burst, and spermatozoa from within are escaping. *a*, *b*, *c*, as in Fig. 29.

FIG. 31.—A transverse section of a sperm-rope, from a series of longitudinal sections of the worm. *a*, *b*, *c*, *d*, as in Fig. 29.

FIG. 32.—View of genital segments of a spent worm, seen by transparency. Drawn from living specimen. *D. v.* Dorsal vessel (the dilatation is not a permanent feature, it merely represents a diastole of the vessel). *G.* Intestine. *ov.* Ovary. *sp. s.* Shrunken sperm-sac, with convoluted blood-vessel on its wall. *spth.* Degenerating spermatheca. *t.* Testis. *v. v.* Ventral blood-vessel.

FIG. 33.—Diagrammatic side view of Psammoryctes, to show arrangement of chætæ.

FIG. 33*a*.—A palmate chæta from dorsal bundle of anterior segments, seen from in front.

FIG. 33*b*.—Same in optical longitudinal section to show curvature of free edge.

FIG. 33*c*.—A multidentate chæta from dorsal bundle.

FIG. 33*d*.—A forked chæta from ventral bundle, anteriorly.

FIG. 33*e*.—A forked chæta from ventral bundle, posteriorly.

FIG. 34.—Diagrammatic side view of Tubifex.

FIG. 34 *a*, *b*, *c*, *d*.—Multidentate chætæ from anterior segments, dorsal bundle, after treatment of the worm with KHO and mounting in glycerine. *b* is a young chæta; the others were in use.

FIG. 35.—A diagrammatic side view of Limnodrilus, Clitellio, and Hemitubifex.

FIG. 35*a*.—A dorsal chæta.

FIG. 36.—A diagrammatic side view of Spirosperma and Ilyodrilus Perrieri.

FIG. 36*a*.—Chæta from dorsal bundle of Ilyodrilus Perrieri.

FIG. 36*b*.—Ditto from other species.

FIG. 36*c*.—Palmate chæta from dorsal bundle of 3rd segment of Spirosperma.

FIG. 36*d*.—Palmate chæta from hinder segments. Same magnification (the lines are too coarse).

FIG. 36*e*.—A ventral chæta.

FIG. 36*f*.—A ventral chæta from one of the anterior six segments.

FIG. 37.—Outlines of chitinous coat of penis of various genera, after Claparède, Eisen, and Vejdovsky. *a*. Hemitubifex. *b*. Telmatodrilus. *c*. Psammoryctes and Spirosperma. *d*. Limnodrilus corallinus. *e*. L. igneus. *f*. L. alpestris. *g*. L. Hoffmeisteri. *k*. L. silvani.

Nais elinguis.

Fig. 38.—The chætæ. *a*. Of dorsal bundle. *b*. A ventral chæta. *c*. A genital chæta.

Fig. 39.—View of genital region from above by transparency (from a living worm compressed). *o*, *o*, *o*. Masses of ova at different stages of development which have dropped away from the ovary. *sp. sac*. Sperm-sac. *spth*. Spermatheca. *ne*. Nephridium.

Fig. 40.—Ventral view of anterior region of sexually mature worm, showing position of clitellum and the genital chætæ (*gen. ch.*). *d*. Dorsal chætæ. *v*. Ordinary ventral chætæ.

Fig. 41.—View of a nearly mature specimen, rather from the side, showing presence of genital chætæ (*gen. ch.*) on one side only. *d*. The still persistent dorsal chætæ of Segment VI. *v*. The still persistent ventral chætæ of the same segment on one side.

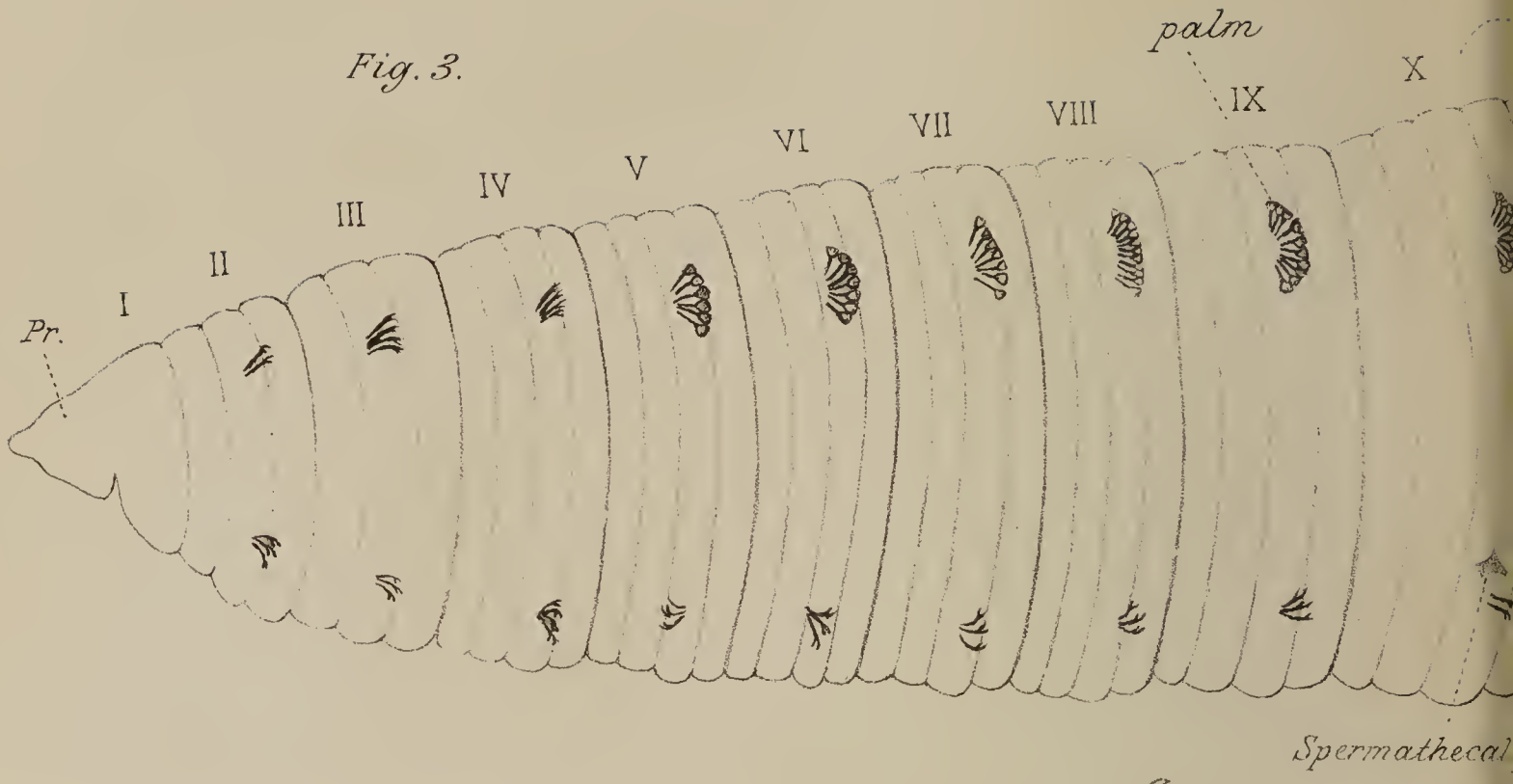
Stylodrilus Vejdovskyi.

Fig. 42.—Ventral view of head. *Pr*. Prostomium.

Fig. 43.—Ventral view of Segments X and XI, to show penis and annulation (*a*, *b*) of the segment. *v*. Ventral chætæ.

Fig. 44.—Chætæ. *a*. From post-genital region, ventral or dorsal. *b*. Pre-genital ventral bundles.

Fig. 3.



Spermathecal

Fig. 4.

Fig. 5.

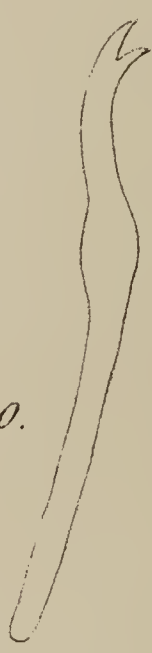
Fig. 7.

Fig. 8.

Fig. 6.

Fig. 9.

Fig. 10.



Dorsal III.

Fig. 11.

Dorsal posterior.

Fig. 12.

Ventral IV.

Fig. 13.

Ventral posterior.

Fig. 14.

Fig. 15.

Fig. I.

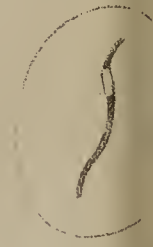


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Fig. 2.

Fig.

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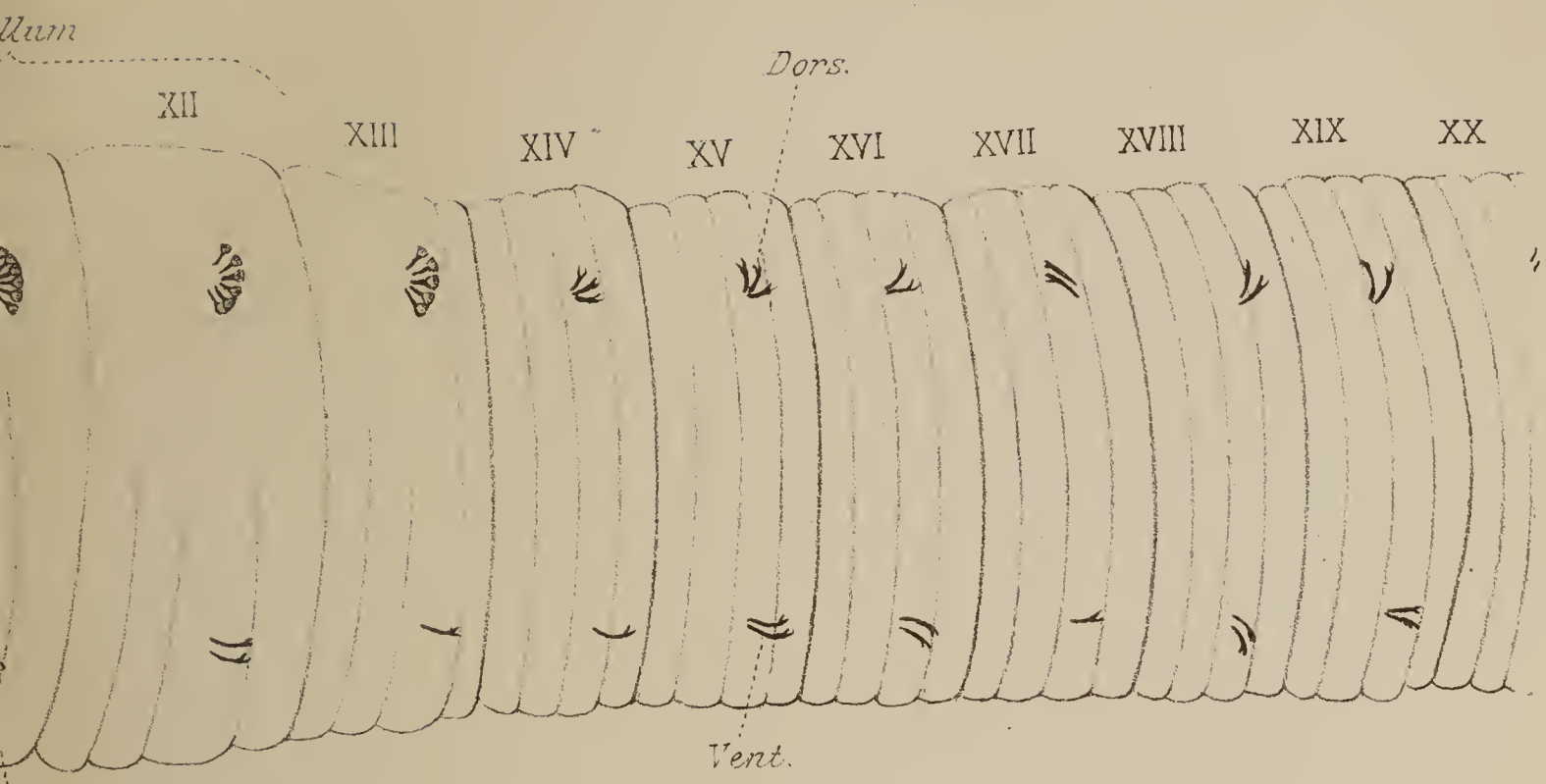

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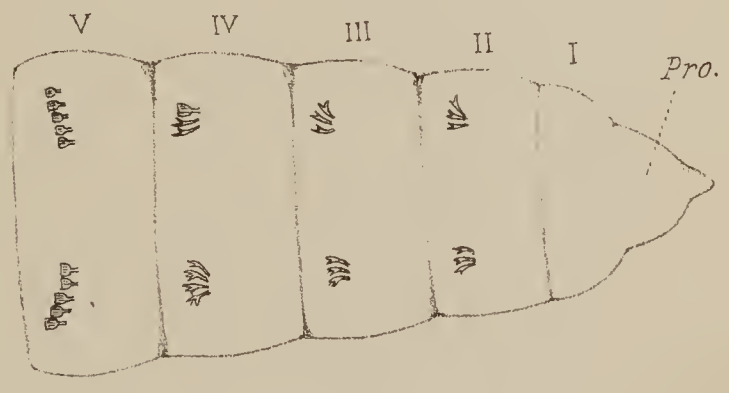

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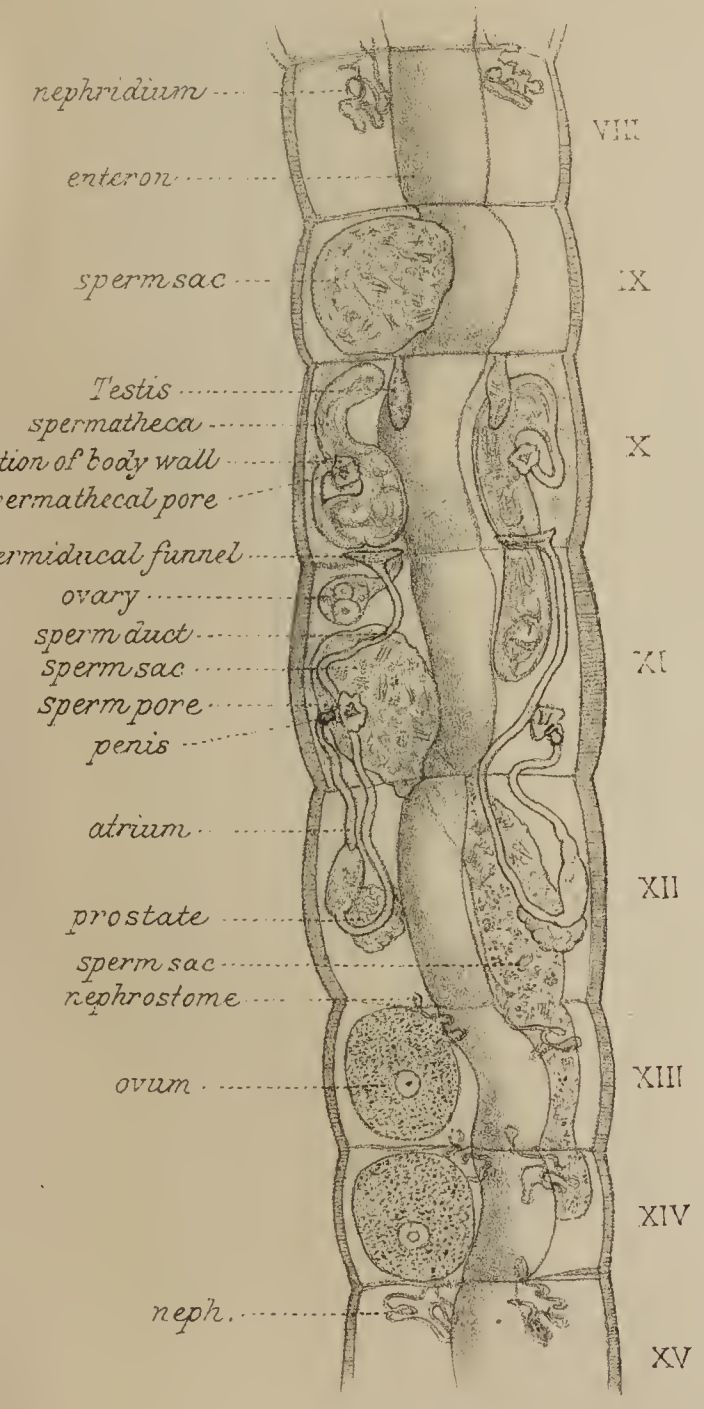

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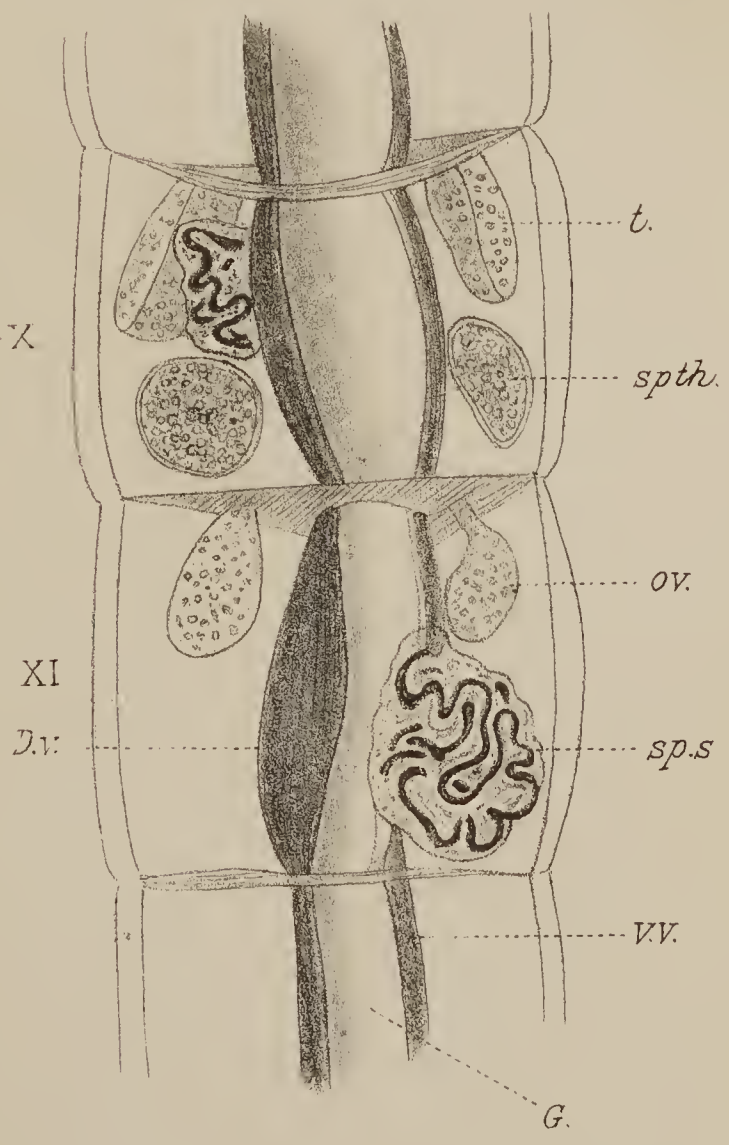

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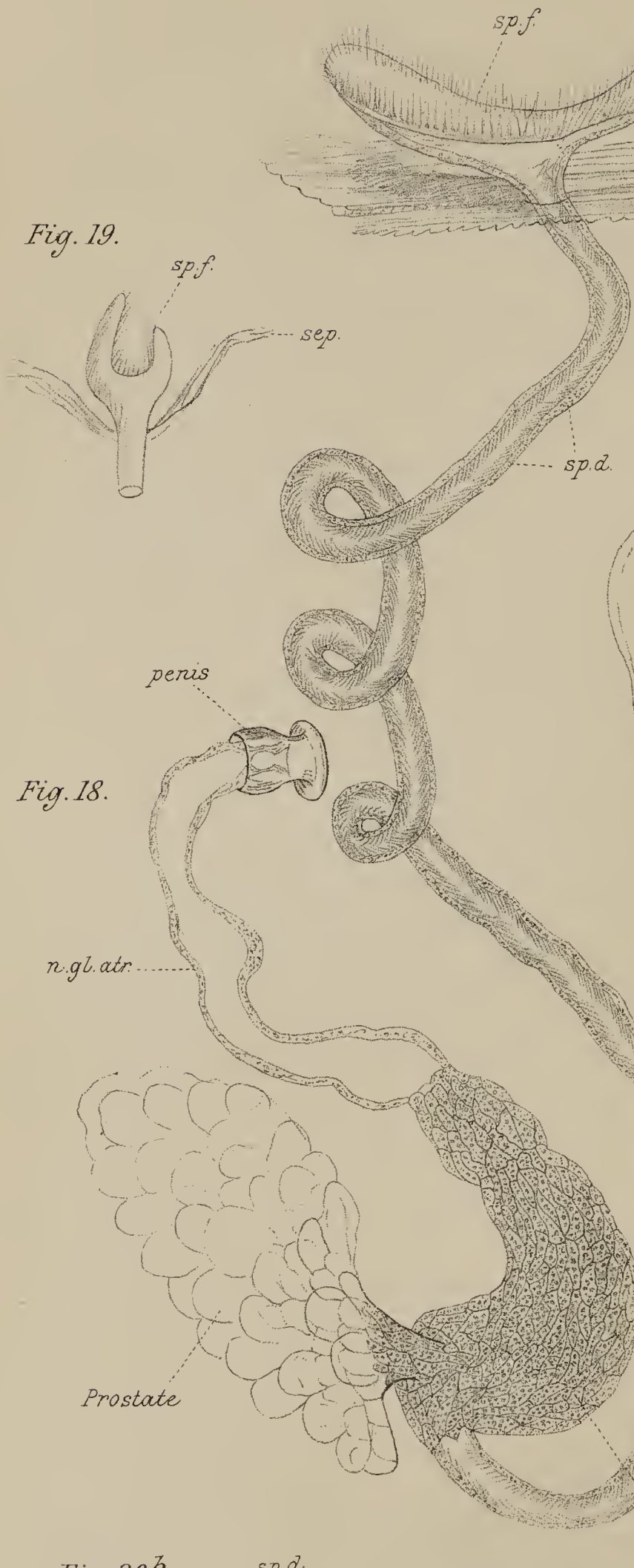

Fig. 19.

Fig. 18.

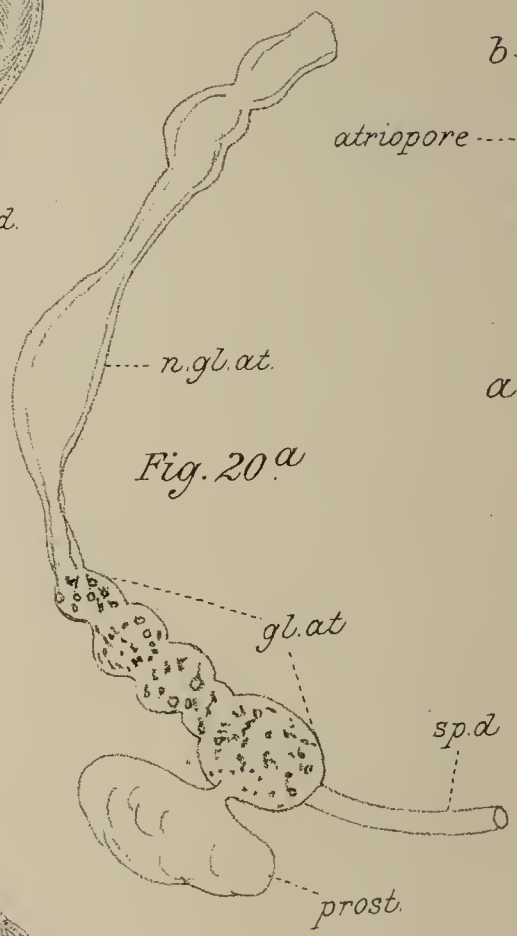

Fig. 20.a

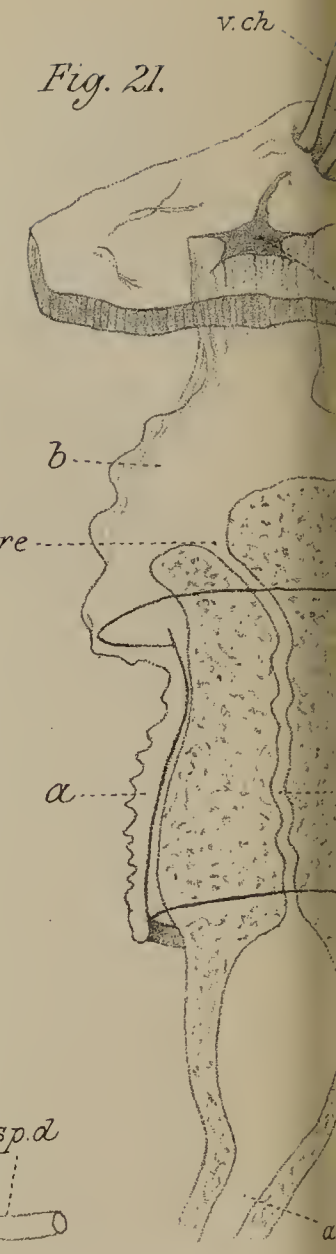

Fig. 21.

Fig. 28.

Fig. 30

c

Fig. 31.

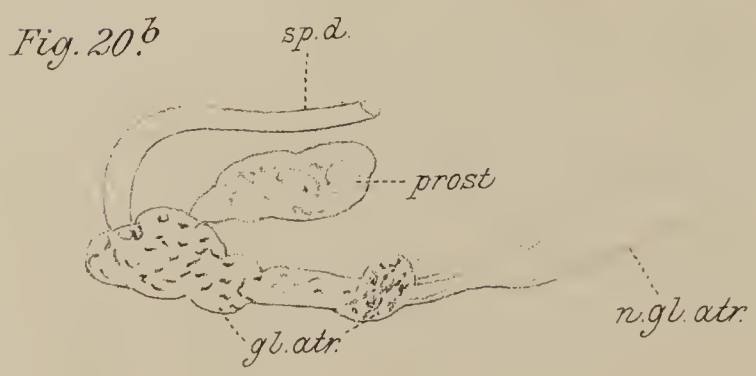

Fig. 20.b

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Fig. 22.

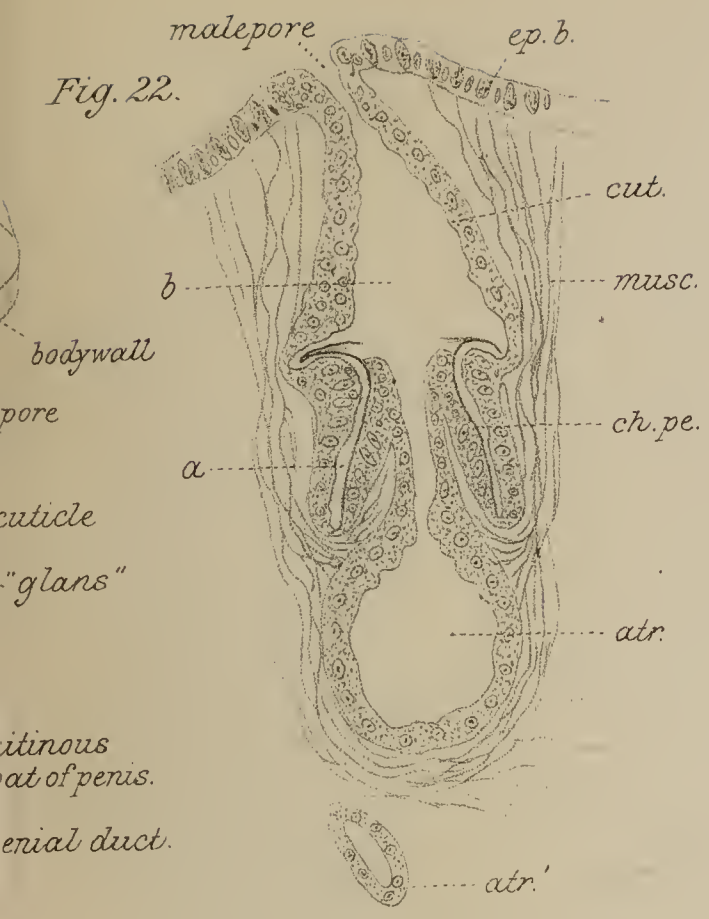

Fig. 27.

Fig. 26.

Fig. 24.

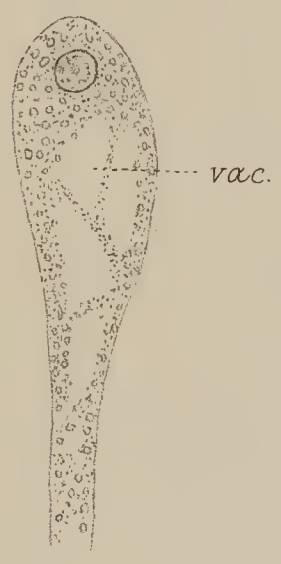

Fig. 25.

Fig. 29.

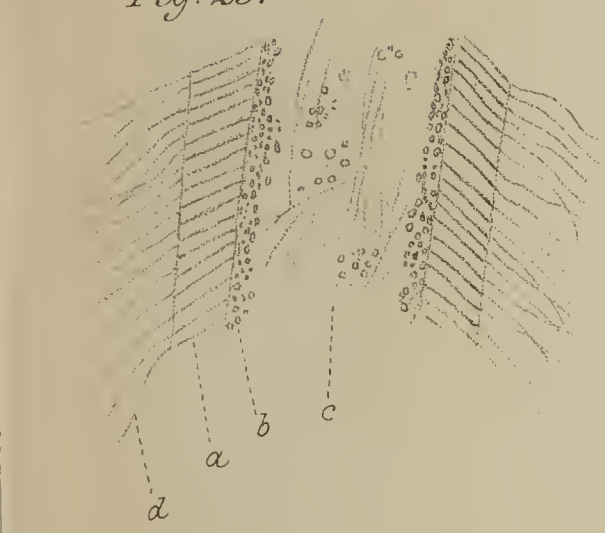

Fig. 23.

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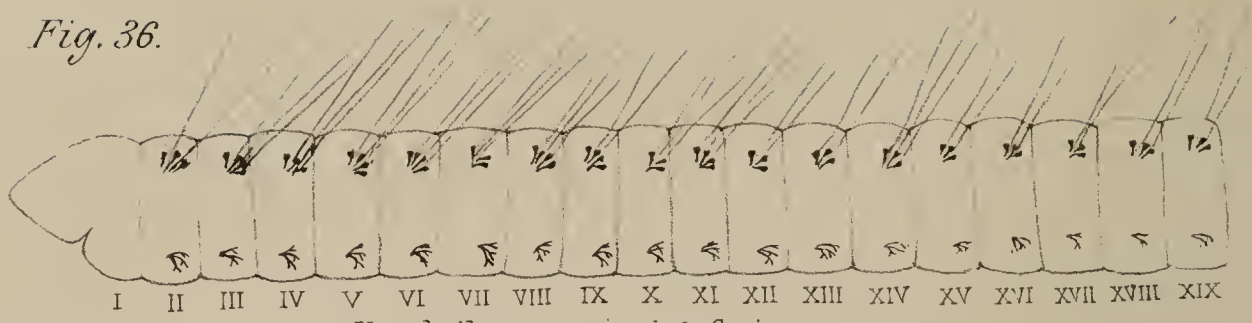
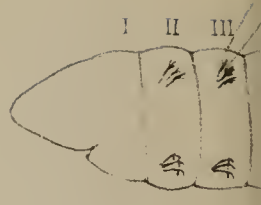
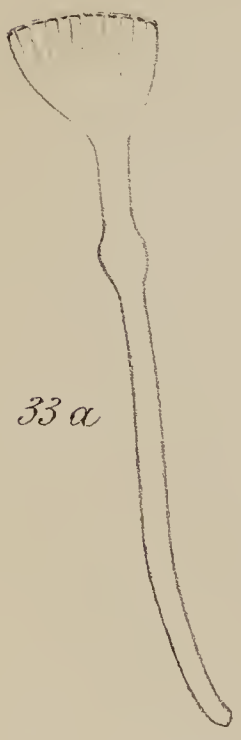
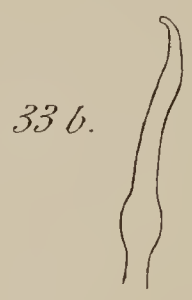
Fig. 36.

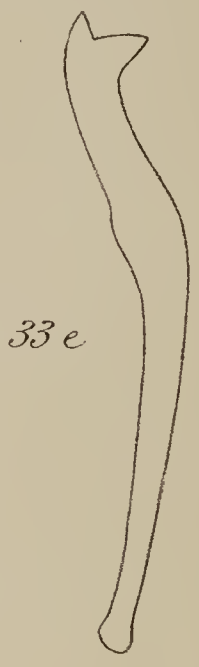


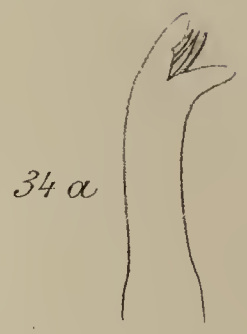


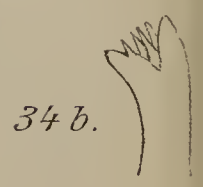
Ilyodrilus perrieri & Spirosperma.

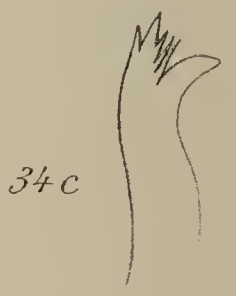












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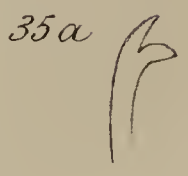
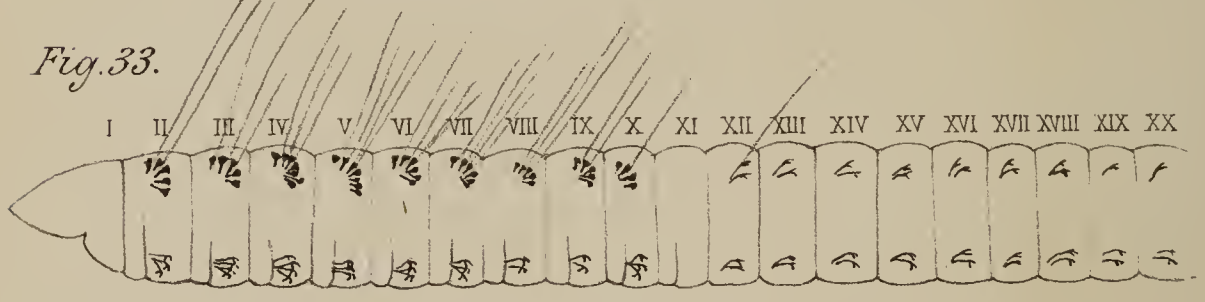
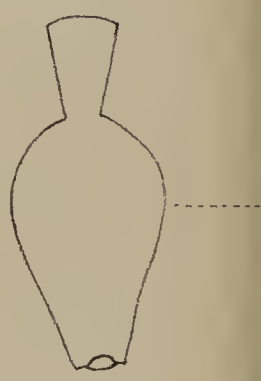


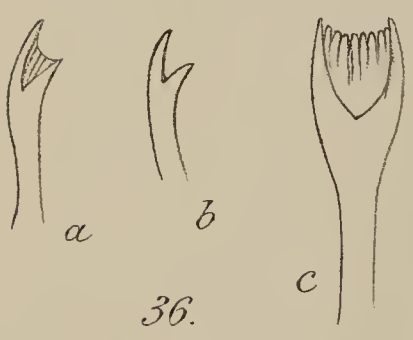
Limnodrilus, Clitellio, Hemitubifex.

Fig. 33.



Psammoryctes.





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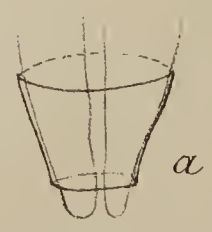
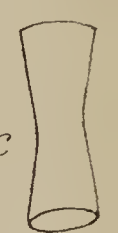


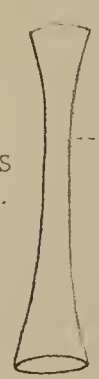
Hemitubifex.

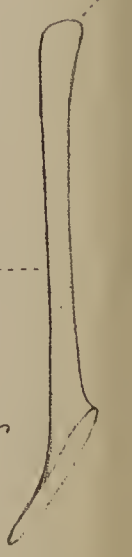
Telmatodrilus.

Fig. 37.



Psammoryctes
Spirosperma.

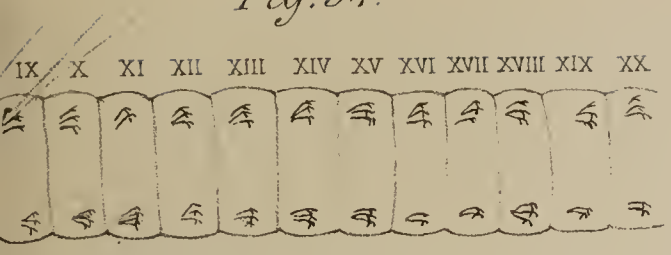




Limnodrilus.

Benham del.

Fig. 34.



Tubifex.

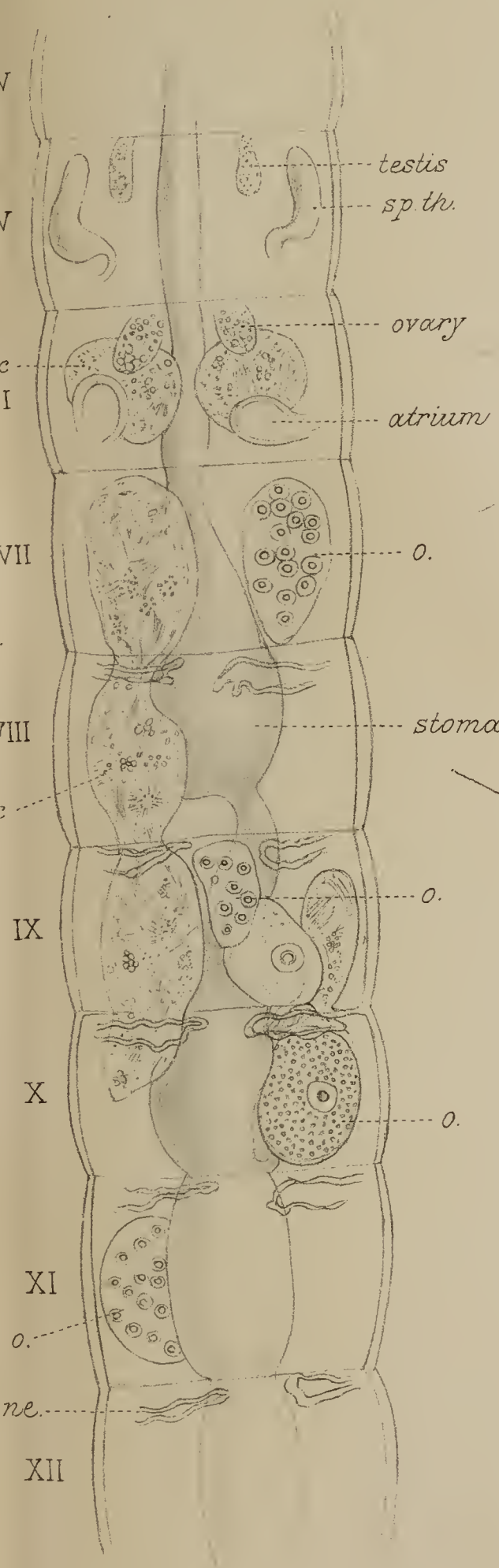


Fig. 38 c

Fig. 38 a

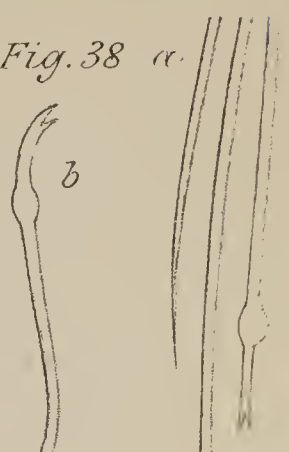


Fig. 40.

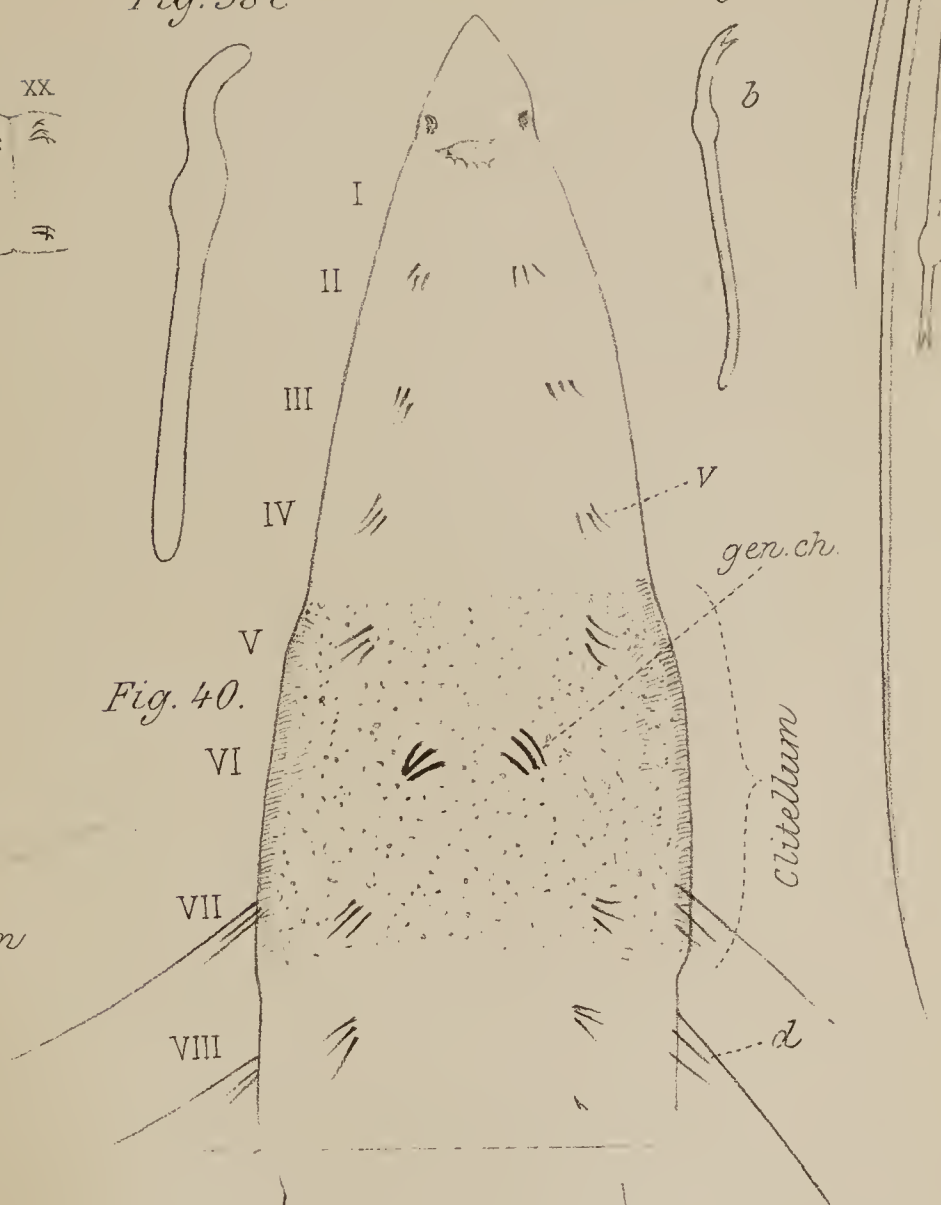


Fig. 41.

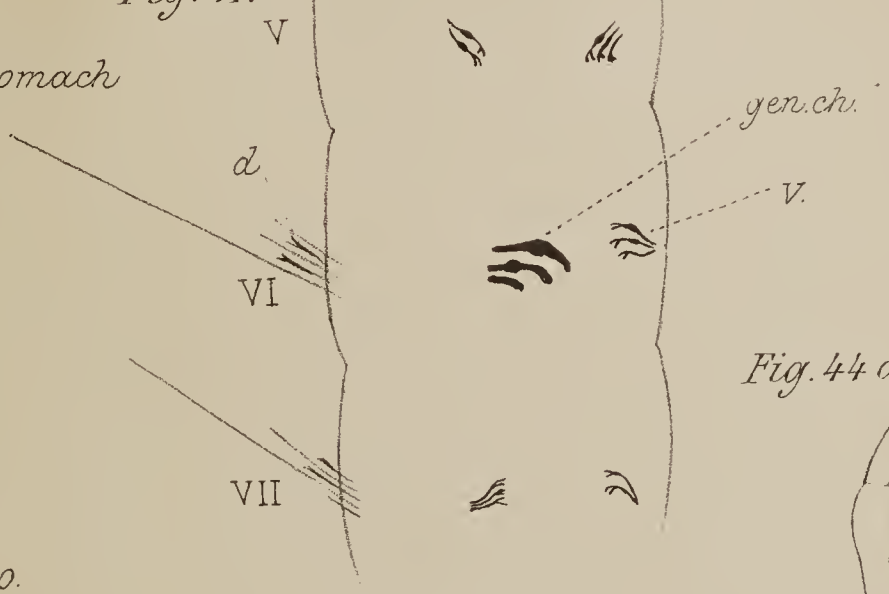


Fig. 44 a

Fig. 44 b

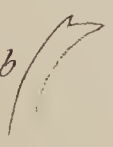


Fig. 43.

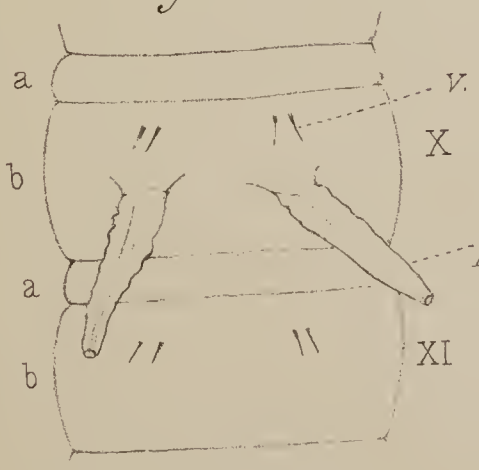
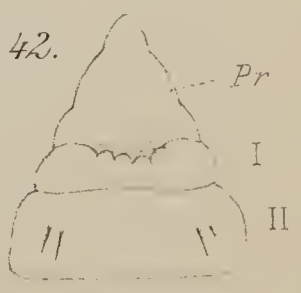


Fig. 42.



F. Huth, Lith^r Edin^r

Note on a Sieve-like Membrane across the Oscula of a Species of Leucosolenia, with some Observations on the Histology of the Sponge.

By

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With Plates X and XI.

At Plymouth, on the rocks immediately beneath the Marine Biological Laboratory, there are to be found at low tide a great number of calcareous and other sponges. Among them occur at least two quite distinct species of Leucosolenia, which can even be distinguished at sight by their mode of growth. The first species, which has only triradiate spicules (genus Ascetta, Haeckel), forms a network of anastomosing tubes, which at first creep close round the seaweeds and other objects, but finally, in large specimens, form great white masses of as much as two inches or more in height. From the network of tubes arise here and there the chimney-like oscula, which are simply continuations of the tubes, and not marked out by their greater diameter from them. The diameter of both the oscula and the ordinary tubes may vary within limits, but the diameter of the oscula is, if anything, less (fig. 10), at any rate not markedly greater than that of the tubes. On the other hand, in the second species of Leucosolenia, which has tri- and quadri-radiate spicules (genus Ascaltis, Haeckel), the mode of growth is essentially the same, but the oscular tubes are at once marked off from the remainder of the sponge by their very much larger size

and greater diameter. They arise at intervals from the comparatively minute basal tubes, as if from a creeping stolon. Both species are of a pure white colour. The second of the two species is, without doubt, Leucosolenia botryoides (Ellis and Sol.), Bwk., the Ascaltis botryoides, var. Ellisii, of Haeckel. The first, or Ascetta species, I have more difficulty in identifying. Fig. 14, *a*, *b*, *c*, represents some of its spicules. As may be seen, they are precisely similar to the spicule of Leucosolenia coriacea, figured by Bowerbank.[1] On the other hand, they differ somewhat from the figures of the spicules of Ascetta coriacea given by Haeckel[2] in having much sharper points, in which they resemble his figures of the spicules of A. primordialis.[3] In his description of the spicules of A. coriacea Haeckel states that the spicules are "gar nicht, oder nur wenig gegen die Spitze hin verdünnt. Die Spitze ist stets stumpf, niemals scharf, meistens glatt abgerundet," &c.[4] This description does not apply well to the spicules here under consideration; still less, however, does the description "schlank conisch," applied to the spicules of Ascetta primordialis, suit them. They have much more cylindrical rays than the spicules of A. primordialis. Since, moreover, A. primordialis is said to be wanting on the Atlantic coasts, and to be replaced there by A. coriacea,[5] this sponge may stand, for the present at any rate, as Leucosolenia coriacea (Montague), Bwk., the Ascetta coriacea (Tarropsis form ?) of Haeckel. It is in Leucosolenia coriacea, as here identified, that the sieve membrane occurs which I am about to describe. In the summer of 1890 I collected a quantity of this sponge in order to make preparations for teaching purposes. In vertical sections of the sponge passing through an osculum I was at once struck by the appearance of a thin perforated membrane stretched across the

[1] 'Mon. Brit. Spongiadæ,' vol. iii, pl. iii, fig. 14.
[2] 'Die Kalkschwämme,' Bd. iii. Taf. v, figs. 2 *a*—*c*.
[3] 'Die Kalkschwämme,' T. c., Taf. v, figs. 1 *a*—*h*.
[4] Ibid., Bd. ii, p. 30.
[5] Ibid., Bd. ii, p. 27.

opening just above where the collar cells end (figs. 1, 2, 3, 5, 13). Having found no mention of such a membrane in the sponge literature[1] I proceeded to investigate it further, intend-

[1] Haeckel, in his classical monograph 'Die Kalkschwämme,' Bd. i, p. 267, describes, under the name of "Mundhaut oder Oscular-membran," a structure in Sycons and Leucons which resembles somewhat from his description (there are unfortunately no figures) the membrane here described. In the Ascons "ist mir ihre Existenz überhaupt noch zweifelhaft." He writes, "Die Oscular-Membran ist eine dünne, keine Spicula enthaltende Lamelle des Syncytium, welche inwendig von der Basis (dem aboralen oder unteren Rande) des Rüssels oder des Peristom-Kranzes ausgeht. Bei weit geoffnetem Mundcanal wird sie (durch Retraction in das Exoderm) entweder ganz unsichtbar, oder bleibt bloss als ein ganz schmaler Ring stehen. Bei völlig geschlossenem Mundcanal hingegen bildet sie eine sehr zarte transversale Scheidewand, welche senkrecht auf der Längsachse des Magen steht." This membrane of Haeckel's has therefore quite a different structure from that which I describe here, but it has precisely the same relations to the osculum, and may well be homologous with it. It is to be hoped someone will give us before long a fuller description (with figures) of this "Oscular-membran." My friend, Mr. G. P. Bidder, has directed my attention to a passage in the works of Dr. Grant ('Edinburgh Philosophical Journal,' xiii, 1825, p. 381), quoted in Johnston's 'British Sponges and Corallines,' p. 51. "When we cut," says Dr. Grant, "a thin piece off the surface of a living sponge and look down through one of its pores with the reflecting microscope, we perceive, immediately beneath the projecting spiculæ which defend the pore, a very delicate network of gelatinous threads thrown over the entrance of the tube. This piece of structure is so fine as to be perfectly invisible to the naked eye; it consists of five or six threads, which pass in from the sides of the tubes to be connected with a central mesh, so that there are six or seven meshes thus formed; and while this soft apparatus is beautifully defended by the projecting spicula of the pore, it serves still further to guard the interior of the animal from the smallest particles of sand, or the minutest visible animalcules." Since Grant distinguished clearly, both in this work and in others, between "pores" and "fæcal orifices," this network of his can have nothing to do with the membrane I describe here. But Johnston seems to have taken this description as applying to the oscula (T. c., p. 53, foot-note), and reminds his readers that Grant's description can apply to the oscula of one or two species only. He adds that "in general the oscula are merely simple or compound outlets, without any protective net over the orifice or in the funnel; and indeed it can rarely be seen except in newly formed oscula before the fibres of the sponge have been broken away by the effluent current"—a most noteworthy statement.

ing at the same time to thoroughly work out the anatomy and histology of this and other Plymouth species of Leucosolenia. As, however, I was obliged to leave England for Naples at an early stage of my investigations, I thought it best to publish an account of this membrane at once, together with a few scattered observations on the histology of the sponge, hoping at some future time to make a more complete study of this interesting sponge genus.

In a typical osculum the interior of the chimney-like tube is seen in sections to be lined by a layer of collared epithelium, only interrupted at intervals by the openings of pores (fig. 1). At a certain height the layer of the collar cells stops abruptly, but the wall of the oscular tube is continued on for a short distance as a funnel-like expansion ("rüsselformige Mundöffnung") consisting of jelly containing spicules and lined by ectoderm. Immediately above the layer of collar cells the sieve membrane stretches across the opening. It is thus some distance below the actual margin of the oscular opening. Figs. 1, 2, 3, 12 *a* and *b*, and 13 show the membrane in section. Figs. 6 and 9 represent portions of it macerated out in glycerine, the portion in fig. 1 having been previously treated with weak acetic, and that in fig. 9 stained in picrocarmine. Fig. 5 shows a side view of a whole osculum (the one from which fig. 6 was dissected out) mounted in glycerine after fixation with osmic and removal of the spicules by dilute acetic. Fig. 10 shows a view from above of a whole osculum mounted in Canada balsam, after having been fixed with absolute alcohol and stained in hæmatoxylin, while 10 *a* represents the entire sieve membrane of the same osculum, drawn with a somewhat low magnification. Finally, fig. 11 *a* and *b* represent two consecutive sections from a series taken across an osculum transversely but slightly obliquely, so that portions of the membrane are obtained flat.

The sieve membrane varies in size, naturally, with the diameter of the osculum. The smallest open osculum I have seen was about 175 μ in diameter, the largest about 465 μ, or nearly half a millimetre. The osculum without any opening

shown in fig. 3, which we shall consider again below, was only about 116 μ in diameter. The sieve membrane is composed of two layers of cells in apposition, but separated by a thin layer of jelly (figs. 2, 3, 12, 13). These cells have a central portion containing the nucleus, and are continued out into three, four, five, or even six processes, which unite with the processes of other cells, thus forming a network with comparatively wide meshes. The body of the cell forms a node or part of one, bnt not all the nodes of the network are formed thus. Many nodes are formed simply by the union of three cell processes. Thus larger and smaller nodes can be distinguished. The former contain usually (not always) one, two, or even three (fig. 9, *c*) nuclei, and are often of considerable thickness. In a side view (9, *b*) or section (12 *a*, 12 *b*, 13) of such a node the two cells with the jelly between can be easily seen. Round the nuclei are a great number of granules, sometimes large, more often very small, which turn black in osmic, and make the nucleus hard to distinguish in surface views. The best preparations are obtained by fixing with osmic, which preserves the shape of the network, and then staining with picrocarmine, which removes to a great extent the blackening. The nuclei can then be readily seen as small spherical clear bodies (fig. 9, *a*, *b*, *c*), usually with a nucleolus, which is not, however, always visible. In osmic preparations not cleared with picrocarmine, the opacity of the cell makes it almost impossible to see the nucleus (fig. 11, *a* and *b*). In preparations fixed in absolute alcohol the nuclei show up well after staining, but the network seems to shrink a little. From these larger nodes radiate out the fine strands composing the network. Each strand is composed of a very fine core of jelly coated by a delicate prolongation from a granular nodal cell. The smaller, usually triangular nodes are, as already stated, simply formed by the confluence of the fine strand making up the network, and have the same structure. The meshes of the network are approximately equal in size in different membranes; in large oscula there are more openings, in smaller ones fewer.

To resume, then, this membrane may be described as a delicate network composed of two layers of cells with a minute quantity of jelly between them. The inner layer becomes directly continuous with the layer of collared epithelium composing the endoderm of the sponge. I have not observed with certainty any form of cell intermediate between the flattened cell of the sieve membrane and the columnar collared endoderm cell. The round cells often seen at the junction of the two, as in fig. 13, appear to me to be ordinary collared cells cut obliquely. Similar appearances can be seen in any spot where the section is not accurately radial to the wall of the tube. The outer layer of the sieve membrane becomes similarly continuous with the ectoderm. To discuss the morphology of this sieve membrane it is necessary to know the homologies of the layer composing it. Three alternatives are possible; either the inner layer is endoderm and the outer ectoderm; or both layers are ectoderm; or both are endoderm. I think the third hypothesis may be dismissed at once, and that it lies between the first two. The question could only be solved satisfactorily by a study of the development of the membrane, which I have not been able to make, but I believe certain facts point very strongly to the first hypothesis being true, i. e. to the inner layer of the membrane being composed of endoderm, the outer of ectoderm. In the first place, in a growing colony of this sponge, there are two ways in which a new osculum may be formed. The first way is by actual division of an osculum into two. Fig. 2 represents two oscula, recently formed, I have no doubt in this way. It is a process similar to that described and figured by Schulze in Farrea occa,[1] a sponge which grows in a manner very similar to this Ascetta. The second way in which an osculum could arise would be by a cæcal diverticulum growing out from the side of one of the sponge tubes, which after growing to a certain length, becomes perforated distally to form an osculum, very much in the manner in which new individuals are budded in a

[1] "Monograph of the Hexactinellida," '"Challenger" Rep. Zool.,' vol. xxi, pl. lxxii, figs. 1—3.

Hydroid colony. This is, I believe, the commonest method of the formation of new oscula. In fact, I believe that in the other species of Leucosolenia mentioned above, it is the only way in which new oscula are formed, and explains the difference in the mode of growth between the two sponges. Blind diverticula of the tube composing the sponge occur very commonly, and I have observed many such. This method of formation of the osculum is essentially similar to the formation of the primitive osculum in the young sponge after the metamorphosis from the larval condition, when the osculum always arises as a breaking through of the gastral cavity to the exterior. Now in this mode of oscular formation a sieve membrane similar to that here described might be formed in one of two ways. The simplest method would be by the gastral cavity breaking through to the exterior in not one, but several places. The result would be the formation of a sieve-like membrane of two layers, in which the inner layer was endoderm, the outer ectoderm. Or secondly, after a simple wide opening was formed, a ring-like ingrowth of the margin of the osculum might take place towards the centre of the aperture, forming a kind of diaphragm, which, after becoming secondarily perforated, would form a sieve membrane in which both layers of cells might be ectoderm. I strongly believe myself, though I have no direct observations to support my views, that the sieve membrane here described arises in the first method suggested above, as a breaking through in several places of the gastral cavity to the exterior. In fig. 3 is represented one of a series of sections through an osculum, which, besides being of very small size (116 μ in diameter, vide supra), is further marked out by the fact that its membrane has no opening, either in this or in any of the sections, of which my series is perfectly complete. I have also another series of sections through a precisely similar osculum, in which there is no trace of an opening in the membrane. In the osculum represented in fig. 3, of which my sections are very satisfactorily preserved and stained, I noticed three other points. First, I could see no pores at all in the wall of the oscular tube.

Secondly, the collars of the endoderm-cells were comparatively low, not more than one third the height of the cell, while in cells from other parts of the sponge in the same section the collars were more than half the height of the cell, (fig. 4). Thirdly, in the membrane itself, the cells composing it were less granular and opaque, appearing more protoplasmic, with very distinct nuclei. The first two of these points makes it probable that the osculum was not in full functional activity; the third point shows that the cells were in a more primitive and less differentiated condition. Here then is just such an osculum as one would expect to find on the hypothesis that the sieve membrane arises as a breaking through of the gastric cavity to the exterior in several places and that the inner layer of cells composing it is endoderm, derived by flattening out of the collared endoderm-cells, while the outer layer is similarly ectoderm. Unfortunately I have observed no other intermediate stage. A curious point is the projection above the membrane of the wall of the sponge, forming the funnel-shaped expansion mentioned above. Here I may refer to Schulze's well-known figures of the young Sycondra raphanus.[1] These figures represent the young Sycon in an Ascon stage, and one might say that here we had a transitory Leucosolenia, with an osculum covered by a sieve membrane with only a single perforation. Round the edge of the osculum a fringe of spicules projects up. As one knows that projecting spicules in sponges are not really naked, one can easily imagine how from such a condition a rim like that in Ascetta could be formed.

The conclusion is, then, that the sieve membrane we are here concerned with is formed by the gastral cavity breaking through to the exterior in several places during development, and that its inner layer of cells is endoderm, the outer layer

[1] 'Zeitschr. f. wiss. Zool.,' xxxi (1878), Taf. xix, figs. 12, 13; or see Vosmaer, 'Porifera' (Bronn's Thierreich), Taf. xxxi, figs. 9, 10; Balfour, 'Comp. Embr.'

From the condition figured by Schulze might easily arise either a sieve membrane or an oscular sphincter, or an "Oscular-membran."

ectoderm—a conclusion which, it must be confessed, is still in need of further developmental facts to raise it above the rank of a probable hypothesis. If now we go further afield, and try to find something with which to compare it, we are at once struck by the great resemblance it presents, in many points, to the sieve plates of Euplectella, Holascus, and Hyalonema, among Hexactinellida. In fact, Schulze's figure[1] of Euplectella suberea, Wyv. Thomson, looks at first sight almost as if it had been drawn from a preparation of my Ascetta. But of course there is an enormous difference between the two, not only in size, but in structure, since the membrane of Euplectella is mostly made up of spicules. In the sieve membrane of Ascetta, however, there is a thin layer of jelly between the two layers, and it is not very difficult to imagine how this layer might be invaded by scleroblasts, and come to contain spicules. It is evident that, if the gastral cavity and osculum of Ascetta were to grow to the size of that of Euplectella, a support of spicules would be necessary for the sieve membrane, and doubtless would be acquired. If this homology between the oscular sieve membrane and plate of Ascetta and Euplectella respectively be true, it would show that the osculum of Euplectella is a true osculum, and its gastral cavity a true gastral cavity,[2] since it can hardly be

[1] Schulze, 'Monograph of Hexactinellida,' pl. v, fig. 1.

[2] Apart from any considerations about the oscular sieve plate there can hardly be any doubt that the internal cavity of a sac-like Hexactinellid is a true gastral cavity, especially if one considers the young forms figured by Schulze on pl. liii, and also on pl. lxii, fig. 5, of his beautiful monograph. Schulze has further shown in the clearest manner how this simple gastral cavity may become modified. "By the expansion of the upper oscular margin many species acquire a funnel-like shape. A further widening and flattening leads to the formation of a flat saucer-like body, while a more unilateral growth results in an ear or shell-like form, . . . or even in certain circumstances in a simple perpendicular plate-like form." "If the outer margin of a stalked or originally cup-shaped sponge becomes folded outwards and downwards through great development of the median portion, a fungoid form arises. . . . In this way, then, as the gastral cavity and osculum have thus been lost, what was originally the internal gastral has become the upper and outer surface, so that the water enters the body from below and escapes

doubted that the osculum and gastral cavity of Ascetta are such. But it is a far cry from Leucosolenia to Euplectella, and no amount of similarity in structural relations will

again from the upper surface," and so on (Schulze, 'Mon. of Hexact.,' pp. 21, 22). What then must be our astonishment, after reading these words, to find Von Lendenfeld, in his 'Monograph of the Horny Sponges,' quietly putting down the gastral cavities of Hexactinellids as preoscular spaces, or even as pseudoscular, a name which he applies to entrances to the inhalent system (l. c., p. 739)! "In the tubular Euplectella aspergillum and in allied forms the central cavity, considering the wall of such a tube homologous to the lamella of the cup-shaped or irregular flattened forms, appears as a preoscular tube, so that here also there are no proper exhalent canals [I must confess to finding some difficulty in understanding this conclusion]. Thus, roughly speaking, all Hexactinellids are lamellæ, and the exhalent canal system is represented by a continuous cavity pervaded by lamellæ. The chambers open into one side of it, and the oscula are situated in the opposite wall" (l. c., p. 717). And this from an author who can only have obtained such knowledge of the Hexactinellids as he possesses from reading Schulze's monograph, and who has not a particle of evidence to support his view! nor, indeed, does he attempt to give us any. One more instance of Dr. von Lendenfeld's homologies may well be discussed here, since it concerns the oscular sieve-plate. On p. 720 of his monograph of the 'Horny Sponges' we find it stated in the description of Dendrilla cavernosa that "the terminal parts—pseudoscula—are covered over by fine sieves with circular pores 0·2 mm. wide, which can be entirely closed at the will of the sponge;" and on p. 758 of the same work we find that Dr. von Lendenfeld "does not hesitate to compare it ["the cribriform membrane which is stretched over the wide terminal pseudoscula of Dendrilla cavernosa"] directly to the terminal sieve of Euplectella aspergillum." This sounds very well; but if we now turn to the more detailed description of this sieve in Dendrilla cavernosa given in Dr. von Lendenfeld's "Studies on Sponges and the Vestibule of Dendrilla cavernosa" ('Proc. Linn. Soc. New South Wales,' vol. x, 1886, pp. 557—561), we learn that "the cavity covered by the pore sieve is a pseudogaster, no oscula are found in its surface; it is a vestibule belonging to the inhalent system" (p. 557). Consequently the gastral cavity of Euplectella belongs to the inhalent canal system; but the chambers of Euplectella open, directly or indirectly, towards this gastral cavity, which leads to the astounding result that the chambers of Euplectella are turned the wrong way! A new kind of inversion of the layers! I am sure it is quite unnecessary to comment further on these fantastic and utterly groundless theories, or to point out the flagrant contradictions in which this author lands himself.

prove absolutely a true homology between the two structures. I should prefer to look upon them as "homoplastic" merely; as agreeing in anatomical relations, and perhaps also in their development and mode of origin, but not as genetically connected. In Calcarea I know of no structure which can be strictly homologised with this membrane, though I think it probable that the "Mundhaut" described by Haeckel, as well as the oscular sphincters, not unfrequent in Calcarea, may be so homologous. Here in Naples I have examined very carefully, by various methods, numerous oscula of Leucosolenia primordialis, but can find no trace of anything resembling the sieve membrane of Leucosolenia coriacea; neither could I in Leucosolenia botryoides.

There is another point about this membrane which is not without importance. Leucosolenia coriacea is a sponge which usually occurs totally devoid of oscula.[1] In Bowerbank's 'Monograph of British Spongiadæ,' vol. ii, p. 35, we read, "Dr. Johnston in treating of this sponge says, 'There are no fæcal orifices.' I have carefully examined a considerable number of specimens with a microscopic power of 160, but have been unable to detect any of the mouths of the cloaca, and attribute this failure to the habit of the animal of closing these orifices at the approach of danger, or while in a state of inaction; and the total absence of internal defensive spicula would seem to indicate the existence of such a power for its protection from its enemies." Haeckel ('Kalkschwämme,' vol. ii, p. 25) writes, "Die bisherigen Beobachter dieses Kalkschwammes haben allerdings fast ausnahmslos nur eine Hauptform derselben beschrieben, nämlich den mundlosen Stock (Auloplegma coriaceum, figs. 27—33)." This "lipostomy" is of common occurrence in many sponges, and according to Haeckel is always found in some Calcarea, e. g.

[1] Ciard found at Wimereux Tarrus, Auloplegma, and Ascometra forms; see 'Bull. Scient. de France et de la Belgique, xxii (1890), part 1, p. 70. But Topsent ("Contributions à l'étude des Clionides," 'Arch. de Zool. expér. et gén.,' v bis, mém. iv) found at Luc only Auloplegma forms.

Ascetta clathrus, Ascaltis cerebrum, &c. Haeckel discusses it at some length, and comes to the conclusion—rightly, I think—that it is "durch Anpassung erworben" ('Kalkschwämme,' Bd. i, pp. 209, 270). He also brings into the discussion the sieve-plate of Euplectella speciosa. I think it is not without interest to find that, in a form most commonly lipostomous, the oscula when present are partially closed by a sieve membrane. Were the opening in this membrane to close up, and the inner layer of cells to become collared cells like the remaining endoderm, lipostomy would be at once attained. The osculum in fig. 3 might be an osculum thus closed; but I believe not, on account of its extremely small size.

In its biological or physiological aspect, I believe this membrane is of use for keeping intruding animals out of the gastral cavity. We can distinguish three ways in which sponges do this. One way is by a fringe of projecting spicules round the osculum, which effectually prevents the ingress of animals into the gastral cavity, though not their exit; e. g. Sycon ciliatum. Other sponges have an iris-like membrane over the osculum, which is sensitive, and can be closed by a sphincter (see Haeckel, 'Kalkschwämme,' Bd. i, p. 266). A third method is by a sieve-plate, as here and in Euplectella, &c. Whether the sieves of Euplectella and of my Ascetta are homologous or not, I have little doubt they are analogous.

On the remaining histology of this sponge I have a few observations to record, though they are not as complete as I could wish. First of all as to the—

Endoderm.—In sections of the sponge hardened in osmic immediately after plucking it from its native haunts, the collar-cells present the appearance of a columnar epithelium composed of cells quite distinct from one another, each with a rounded slightly enlarged base stuck into the jelly and containing the nucleus, while the upper part of the cell is prolonged into a collar about half or two thirds the height of the cell. In the centre of the collar the flagellum is usually

distinct. These cells are best studied either by maceration of carefully fixed portions of the sponge, or by tearing up and examining living pieces. My macerations were done by fixing fresh pieces of the sponge in $\frac{1}{2}$ per cent. osmic acid, and then soaking them in dilute glycerine, with or without previous treatment with $\frac{1}{2}$ per cent. acetic acid or picro-carmine. After a time the cells may easily be separated by taps on the cover-glass with a needle.

The shape of the cell in fresh specimens well hardened in osmic is elongated, as described above, but when teased up alive the cells become rounded (fig. 16), as is also the case in specimens hardened in Flemming's fluid (fig. 22). In the living condition they may be observed to vary in shape, becoming, in fact, amœboid, as has been often observed. In living cells thus treated I have never been able to observe a trace of the collar. It appears to become completely retracted. Here I am in partial agreement with Topsent, who says of the collar-cells of Cliona, "Collerettes et cils sont retractiles comme les pseudopods de cellules améboides."[1] I have always found the flagella quite distinct, but never the collar, though I have no doubt the former are also retractile. This retraction of the collar may be compared to that known to occur in Choanoflagellata.[2] In macerations the collar is sometimes very low (fig. 17), but more often of considerable height (fig. 18). It is usually somewhat crumpled, and appears as two fine lines on each side of the flagellum. It is very seldom that the rim of the collar can be distinctly seen. I never found the collars of neighbouring cells joined together to form a "Sollas's membrane;" I do not say this, however, as a disbeliever in the existence of this structure in some other sponges. I have sections of Halichondria panicea in which I can see it

[1] "Contributions à l'étude des Clionides," 'Arch. de Zool. expér. et gén.,' tome v bis (1887—1890), mém. iv, p. 27.

[2] Bütschli, "Protozoa" in Bronn's 'Thierreich,' Bd. ii, Mastigophora, p. 881: "Wie bekaunt, ist der Kragen, wenigstens bei den Craspedomonadinen, ein gestaltsveränderliches Organ, ja er kann unter Umständen ganz eingezogen, und wiederum neugebildet werden."

distinctly, as described by Dendy.[1] The flagellum is usually about twice the height of the cell, or more. In the cell in fig. 16, which I had under continuous observation for a long time, I noticed that the flagellum made a somewhat slow stroke to the right, followed immediately by a quick stroke to the left, after which there was a pause, and then the two strokes were repeated, and so on. Similar rhythmic pulsations were observed in other cells, and doubtless have to do with causing a current in a definite direction. I observed, also, that when a foreign body came into contact with the end of the flagellum so as to hinder its movements, it stimulated it to greater activity, and caused it to lash about violently so as to become almost invisible, until the foreign body was thrust away, or the cell itself removed from it. When the flagellum was in full swing it appeared thicker at the base than at the tip. But during its pauses it was easy to see that this apparent disparity in thickness was an optical delusion (owing, presumably, to the tip moving more quickly than the base), and the flagellum was really of precisely the same thickness throughout. Similar observations have been made by Clark and Bütschli[2] on the flagella of Flagellata, and these authors have shown that in many species the flagellum, though depicted by earlier writers as tapering towards the tip, was really quite cylindrical. Von Lendenfeld, in his 'Monograph of the Horny Sponges' (p. 777), draws the flagellum of Spongelia distans tapering towards the tip, and at its base sending roots into the protoplasm. I do not wish, however, to cast any doubts (however much I may feel them) on von Lendenfeld's picture, as it was made from a sponge very far removed from Leucosolenia. I never observed any continuation of the flagellum into the interior of the cell. As to cell-contents, I was unable to observe with certainty in the living condition the contractile vacuoles often described. I saw a vacuole frequently, but could

[1] "Studies on the Comparative Anatomy of Sponges:" iv, "On the Flagellated Chambers and Ova of Halichondria panicea," 'Quart. Journ. Micr. Sci.,' Jan., 1891.

[2] Bütschli, "Protozoa" in Bronn's 'Thierreich,' Bd. ii, Mastigophora, p. 673.

not see it contract. But my observations are far from conclusive on this point. The nucleus was best seen in preparations stained with picro-carmine. In other preparations it was often not visible on account of the opacity of the cell. It was always spherical, lodged in the base of the cell, with a distinct cell membrane and nucleolus. In the living condition it was not visible. Besides vacuoles and a nucleus, the cells usually contained pigment granules, which appeared as black specks, both in the living condition and after osmic. They were especially distinct in sections made from sponges hardened in Flemming's fluid and stained with safranin (fig. 22), which tinges them slightly. Sometimes there were very many granules, sometimes none at all. In the living cell these granules were observed to alter in position, but no regular direction of movement was noticed. Only two instances were found of what appeared to be collar-cells in division. In one of these (fig. 18, *e*) no collars could be seen ; the flagella were very short, and no nuclei were visible (after staining with picro-carmine), but the whole cell appeared pinkish—from which, perhaps, it might be inferred that the nuclei were undergoing karyokinesis. In the other instance (fig. 18, *d*) two normal collar-cells were found joined at their base. The only noteworthy point about them was that each nucleus had two nucleoli, not in its centre but at opposite ends, as shown in the figure. I have never found, either in sections or maceration, any process connecting neighbouring collar-cells to one another, though I feel sure they must exist.

Mesoderm.—In macerations I found the spicule to have a nucleus at the extremity of each ray, and a fourth at the confluence of the rays (figs. 15 *a*, *b*). In some sections, especially those prepared with Flemming's fluid followed by safranin, numerous irregular cells of a yellowish colour, and containing a number of black granules but no distinct nuclei, were to be found close under the collar-cells (fig. 22). These are perhaps identical with Topsent's "cellules digestives." I found no trace of muscular, elastic, or other special cells ; nor does there appear to be much occasion for them.

Ectoderm.—I am more in the dark about this layer than about any other part of the sponge. All that was made out with certainty was as follows:—In surface views, after fixing with osmic and removal of the spicules with acid, one sees at intervals patches of black granules (figs. 7 and 8). Some of these are isolated, but most are continuous with the wall of a pore, which also appears granular, either all round or only on one side (see fig. 8; in fig. 7 there are no pores). In maceration the cells appear as seen in fig. 20, where the clear space doubtless represents the nucleus. Fig. 21 represents a single pore macerated out. Each pore appears to be formed of a single ectoderm-cell. In sections the superficial ectoderm-cells sometimes appear as little heaps of granules (fig. 22), but are in general very hard to make out. On the other hand, the granular walls of the pores are easily seen. It is possible that in the fully formed sponge wall the ectoderm-cells may to a certain extent degenerate into a cuticle-like structure.[1] I may

[1] Topsent, in his most important memoir on the Clionidæ already cited, finds that in these forms, the most contractile sponges known, and also in the genera Reniera and Halichondria, it is the flattened epithelial cells of the ectoderm and endoderm clothing the canals, sphincters, &c., that are the real contractile elements (pp. 24—27, 96, &c., and p. 122). He terms them "cellules de revêtement," and states the following important fact: "Sur ces points [i.e. on the papillæ of Cliona] les cellules de revêtement n'auraient pas de raison d'exercer leur contractilité; aussi y sont elles remplacées constamment par une cuticule incolore d'apparence anhiste" (p. 26). The author then cites the observations of Kölliker and Schulze as to a similar cuticle in Cacospongia and Euspongia, &c. Now in our Ascetta the only parts where contraction could take place is round the pores and round the openings of the sieve membrane, and it is precisely in these places that I find the cellular nature of the "cellules de revêtement" most distinct. In other places it has, I believe, degenerated, as Topsent finds. This author's work was not known to me when I made my observations. Metschnikoff, in his "Anatomisches über Ascetta" ('Spongiologische Studien ii, Zeitschr. f. wiss. Zool.,' xxxii, pp. 358—362, Taf. xxii), finds the ectoderm very distinct in A. blanca, primordialis, and clathrus; and is astonished that earlier writers (Haeckel, Oscar, Schmidt, and Keller) could not see it. He figures distinct epithelial cells (figs. 9—11), but these are from Olynthus forms, in which he finds the ectoderm "noch stärker und auffallender ausgebildet als bei den obenerwähuten Tarrusformen." It seems to me probable that

add that neither in the living nor preserved condition could I observe any trace of the flagella described by von Lendenfeld as present in all calcareous sponges ('Descriptive Catalogue of Sponges in the Australian Museum,' Introduction, p. vi), and for my part I feel very sceptical as to their existence.

A few words in conclusion as to the mode of life of this sponge. I have only found it between tide-marks in rock pools. So delicate a creature appears to shelter itself from the violence of the waves by creeping down in amongst the stems of the calcareous algæ, &c. I have frequently pulled up a colony of Styela and found a rich ramification of the sponge tubes round the bases of the Ascidians. Hence it is a very inconspicuous form, and one may look into a pool full of it without observing any until one pulls up and examines the seaweeds closely. In one pool I found it specially abundant. This was a pothole about a foot and a half across, and about two feet deep; the side towards the sea was concave and overhanging, the other sides more or less straight, but all round there was a thick growth of weeds. Here, well sheltered from the waves which must beat over the spot four times in the twenty-four hours, the sponge attained the greatest development I have seen. Nearly every bit of weed was clothed with it, while under the overhanging seaward edge the sponge came out, as it were, from the seaweeds and formed the large masses mentioned at the commencement of this paper.[1] This pool

Metschnikoff had before him a young and undifferentiated form of the ectoderm. It would be of great interest to trace the modifications of the ectoderm during the growth of a single form.

[1] In Sorrento my friend Dr. Otto Maas and I observed a very similar pothole at the entrance to one of the grottes, situated just at the water's edge where the waves were constantly beating into it. This pothole also had the side towards the sea deeply concave, and what made it specially interesting was the fact that under the overhanging edge were growing a large number of specimens of a calcareous sponge (probably Sycandra raphanus; at any rate a Sycon) of various sizes, while the other sides of the pool were bare, except for a few weeds. Dr. Maas has observed, in his valuable paper on the development of Spongilla ('Zeitschr. f. wiss. Zool.,' Bd. l, 1890), that the larvæ avoid the light; and other sponge embryologists have observed the same thing so often, that one is justified, I think, in putting down this habit of

was most convenient to me, as I was able at low tide to go down with a bottle of hardening reagents and preserve pieces of the sponge perfectly fresh from its native habitat, or in five minutes I could have fresh living pieces on the laboratory table. It was remarkable that I found no specimens of Leucosolenia botryoides in this pool, though it occurred in the very next pool to it, both species growing side by side.

Before concluding it is my pleasant duty to express my best thanks to the committee of the British Association for appointing me to one of their tables in the Marine Biological Association Laboratory during three months of the summer of 1890, when I made the bulk of these observations; to my friend Mr. Walter Garstang, then Assistant to the Director of the Marine Biological Association, for a great deal of help and advice; and, finally, to the delegates of the Common University Fund, Oxford, for appointing me to the Oxford table in the Naples Zoological Station, where I have been able to add a few observations to those made at Plymouth.

Addendum.

Since the above was written two works have appeared by Dendy which I must notice. In his 'Organisation and Classification of the Calcarea Homocœla, with Descriptions of the Victorian Species' ("A Monograph of the Victorian Sponges," part 1, 'Transactions of the Royal Society of Victoria,' vol. iii, part 1, 1891), Dendy finds "that the ectoderm of the Homocœla agrees precisely with what Schulze has described for Sycandra raphanus, and what he himself found and described for Grantia labyrinthica. Except in very well-

avoiding the light and seeking the darkest places as a well-marked characteristic of sponge larvæ. Now, in potholes like the two here mentioned, the larvæ by avoiding the light would either settle under the overhanging edge, or down amongst the seaweeds. On the other hand, those that did not do so would inevitably be smashed by the waves. Hence it is probable, I think, that with more extended observations one could give a simple explanation of this habit, as well as a beautiful instance of the power of natural selection in producing it.

preserved specimens it is a matter of great difficulty to make out satisfactorily the structure of the ectodermal epithelium." In carefully prepared sections "the ectoderm generally appears . . . as a delicate but sharp outline, with a moniliform or beaded appearance, due to the swelling caused by the presence of the nucleus in the centre of each cell." The author then figures and describes the ectoderm in Leucosolenia Wilsoni, n. sp. I never saw such distinct cells in L. coriacea, but I have already expressed my opinion above that the structure of the ectoderm varies at different ages. The collar-cells figured by the author from Leucosolenia proxima on pl. viii, figs. 3 and 4, are unlike any I have seen in L. coriacea, but it is possible that they vary in shape in different species. The mesodermal network described by the author in the gastral cavities of L. proxima and Wilsoni (p. 13, pl. viii, figs. 1 and 2) is very remarkable, and reminds one at first sight of the sieve membrane described here; but from the description of the network there can be no real comparison between it and my sieve membrane.

In his "Preliminary Account of Synute pulchella, a New Genus and Species of Calcareous Sponges" (Dendy, 'Proceedings of the Royal Society of Victoria,' March 12th, 1891), the author mentions that "each gastral cavity has also a single large well-developed diaphragm situate just within the osculum" (p. 3). As far as one can judge from the description, this diaphragm may well be homologous with my sieve membrane in Leucosolenia coriacea.

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EXPLANATION OF PLATES X and XI.

Illustrating Mr. Edward A. Minchin's "Note on a Sieve-like Membrane across the Oscula of a Species of Leucosolenia, with some Observations on the Histology of the Sponge."

ect. Ectoderm. *end.* Collared endoderm. *s. m.* Sieve membrane. *G. c.* Gastral cavity. *p.* Pores. *n.* Nuclei. *sp. sh.* spicule sheath.

PLATE X.

Fig. 1.—Vertical section of an oscular tube. Osmic and hæmatoxylin. Zeiss, oc. 2, obj. B.

Fig. 2.—Vertical section of an osculum which has just divided into two. Osmic, picro-carmine, and hæmatoxylin. Zeiss, oc. 4, obj. D. $\frac{152}{1}$.

Fig. 3.—Vertical section of a small oscular tube, in which the sieve membrane was without any opening. There are no pores to be seen in the walls of the tube, and the collars of the endoderm-cells are very low. Osmic, picro-carmine, and hæmatoxylin. Zeiss, oc. 4, obj. D. $\frac{210}{1}$.

Fig. 4.—Collar-cells from another part of the same section as Fig. 3, to show the normal height of the collars relatively to the cells. Zeiss, oc. 8, obj. F, apochrom. $\frac{285}{1}$.

Fig. 5.—Side view of an oscular tube, seen as a transparent object. Osmic half per cent., acetic acid half per cent., glycerine. Zeiss, oc. 2, obj. B.

Fig. 6.—A portion of the sieve membrane of the osculum drawn in Fig. 5, dissected out. Zeiss, oc. 8, obj. F, apochrom. $\frac{400}{1}$.

Fig. 7.—A portion of the wall of the oscular tube above the sieve membrane, from the osculum drawn in Fig. 5. Zeiss, oc. 8, obj. F, apochrom.

Fig. 8.—A portion of the wall of the sponge from below the sieve membrane. From the osculum drawn in Fig. 5. The spicule sheaths are barely visible on account of the opacity of the preparation. Zeiss, oc. 8, obj. F, apochrom.

Fig. 9.—Portions of the sieve membrane of an osculum, dissected out to show the nuclei in the nodes. Osmic half per cent., picro-carmine, glycerine. Zeiss, oc. 8, obj. F, apochrom.

Fig. 10.—View of an osculum looked at from above, showing the sieve membrane, partly hidden by the edge of the aperture, stretched out over the oscular opening. Absolute alcohol, hæmatoxylin. Zeiss, oc. 2, obj. B. $\frac{90}{1}$.

Fig. 10*a*.—The whole of the sieve membrane of the same specimen. Zeiss oc. 4, obj. C.

PLATE XI.

FIGS. 11*a* and *b*.—Two consecutive sections taken across an osculum transversely but slightly obliquely. Osmic 1 per cent., hæmatoxylin. Zeiss, oc. 8, obj. F, apochrom. $\frac{370}{1}$.

FIGS. 12*a* and *b* (Plate X).—Two sections of nodes of the sieve membrane, showing nuclei. $\frac{258}{1}$.

FIG. 13 (Plate X).—Section of sieve membrane, passing throughi ts origin from the wall of the osculum and four nodes. Zeiss, oc. 8, obj. F, apochrom, $\frac{487}{1}$.

FIGS. 14*a*, *b*, and *c*.—Three spicules. $\frac{310}{1}$.

FIGS. 15*a* and *b*.—Two spicules macerated out in glycerine, showing nuclei. Osmic half per cent, picro-carmine, glycerine.

FIG. 16.—Two drawings of an isolated living collar-cell. Zeiss, oc. 8, obj. F, apochrom.

FIG. 17.—A collar-cell from a preparation made with half per cent. osmic, and macerated out in glycerine.

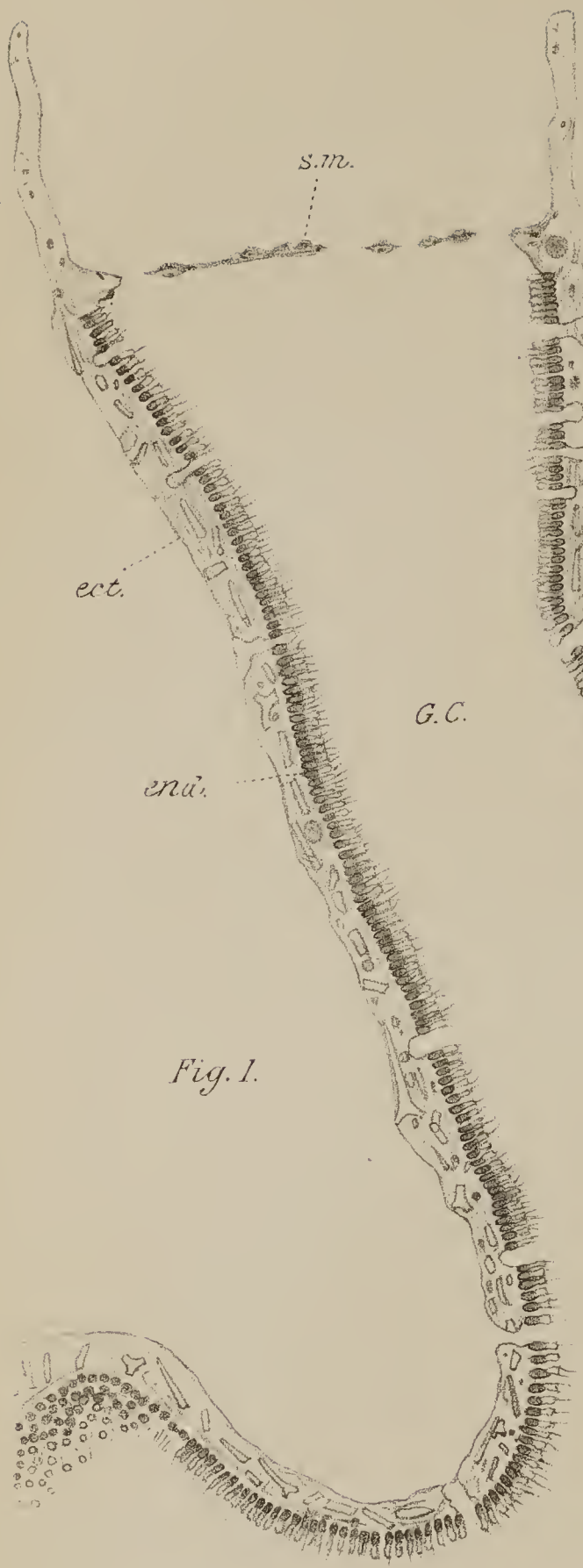
FIG. 18.—Collar-cells from a preparation fixed with half per cent. osmic, stained in picro-carmine, and macerated out with weak glycerine. Two of them are dividing. Zeiss, oc. 8, obj. F, apochrom.

FIG. 19.—Collar-cells macerated out from the same preparation as Figs. 5—8. Zeiss, oc. 8, obj. F, apochrom. $\frac{365}{1}$.

FIG. 20.—An ectoderm-cell. Osmic half per cent, glycerine.

FIG. 21.—A pore macerated out, from the same preparation as Figs. 9*a*, *b*, *c*.

FIG. 22.—Section of the wall of the sponge. Flemming's fluid, hæmatoxylin, safranin. Zeiss, oc. 4, obj. D.



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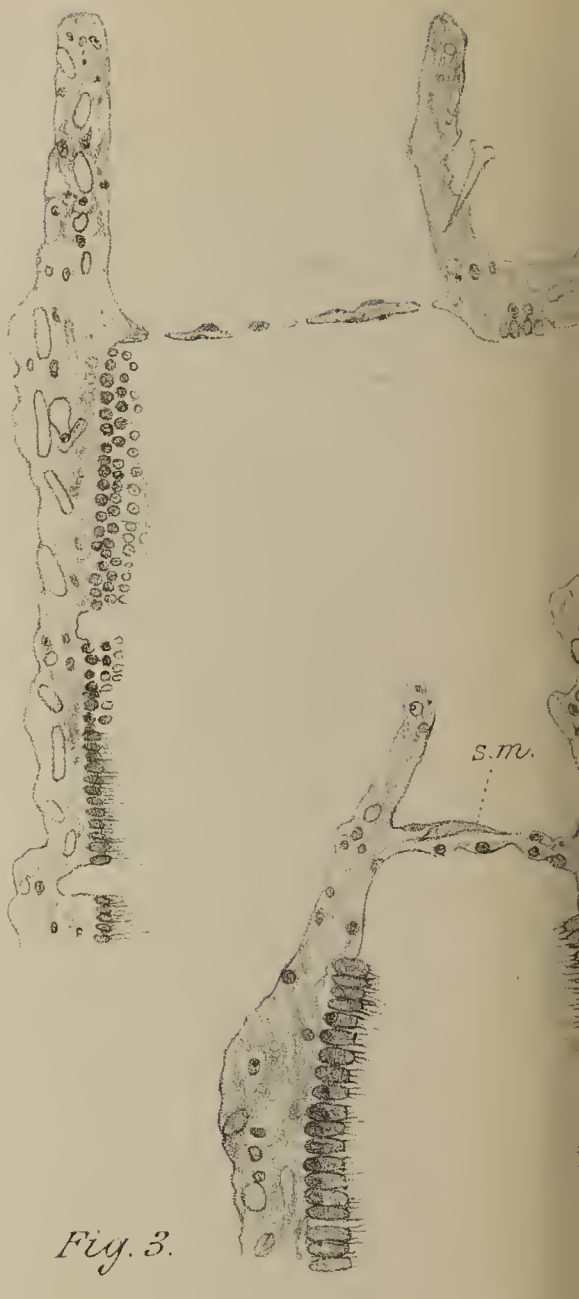

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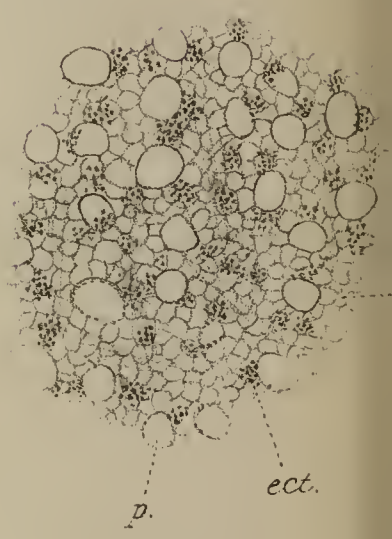

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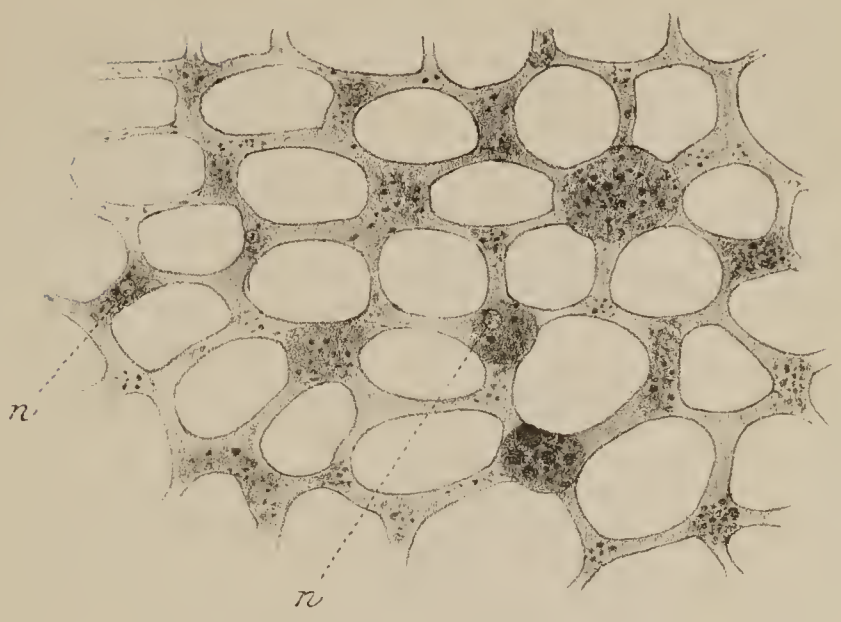

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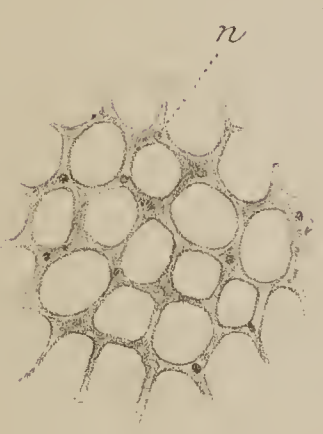

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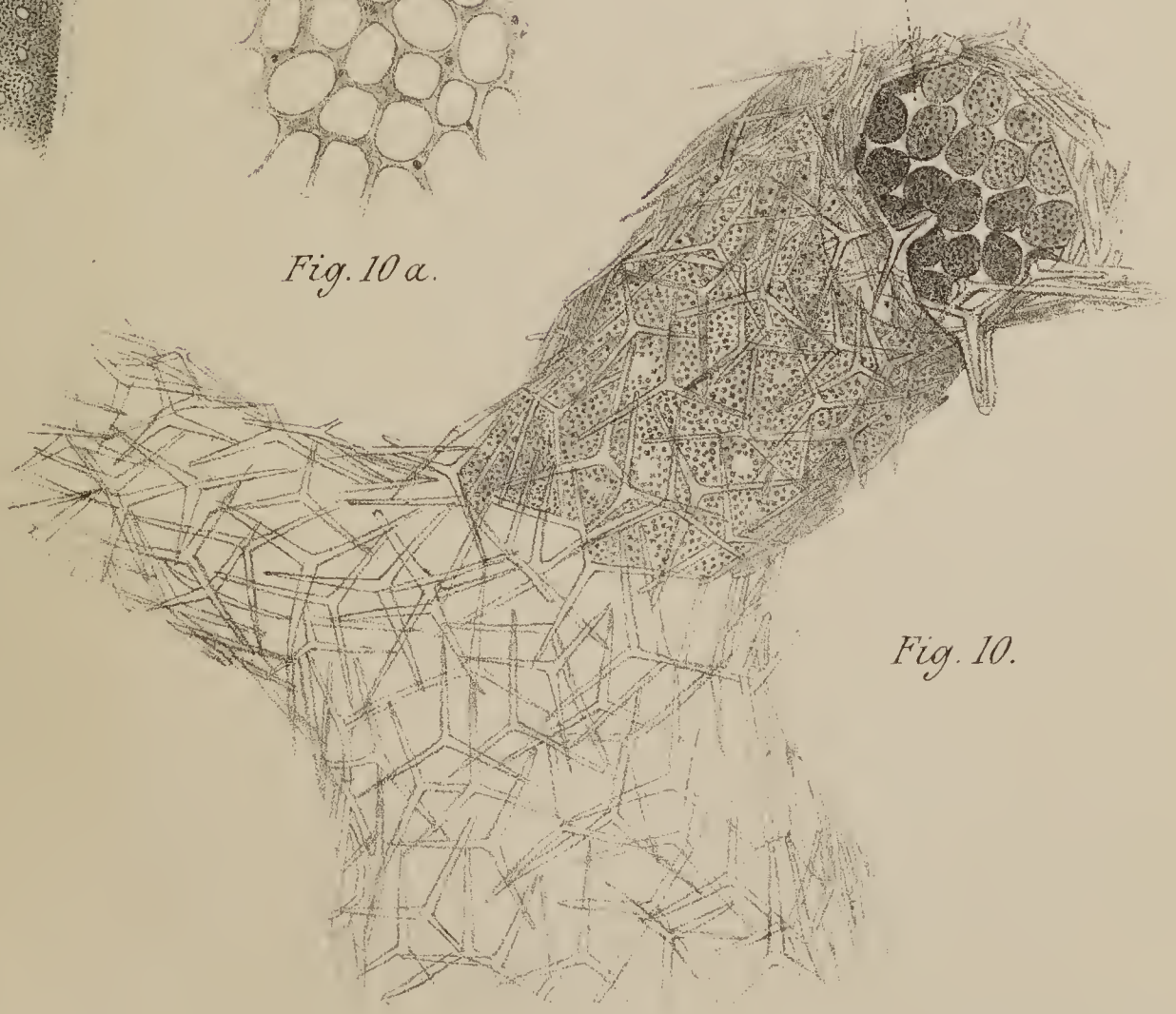

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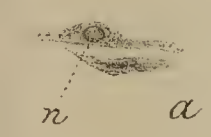

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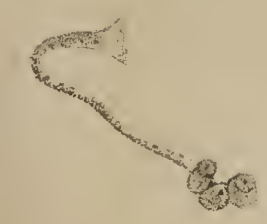

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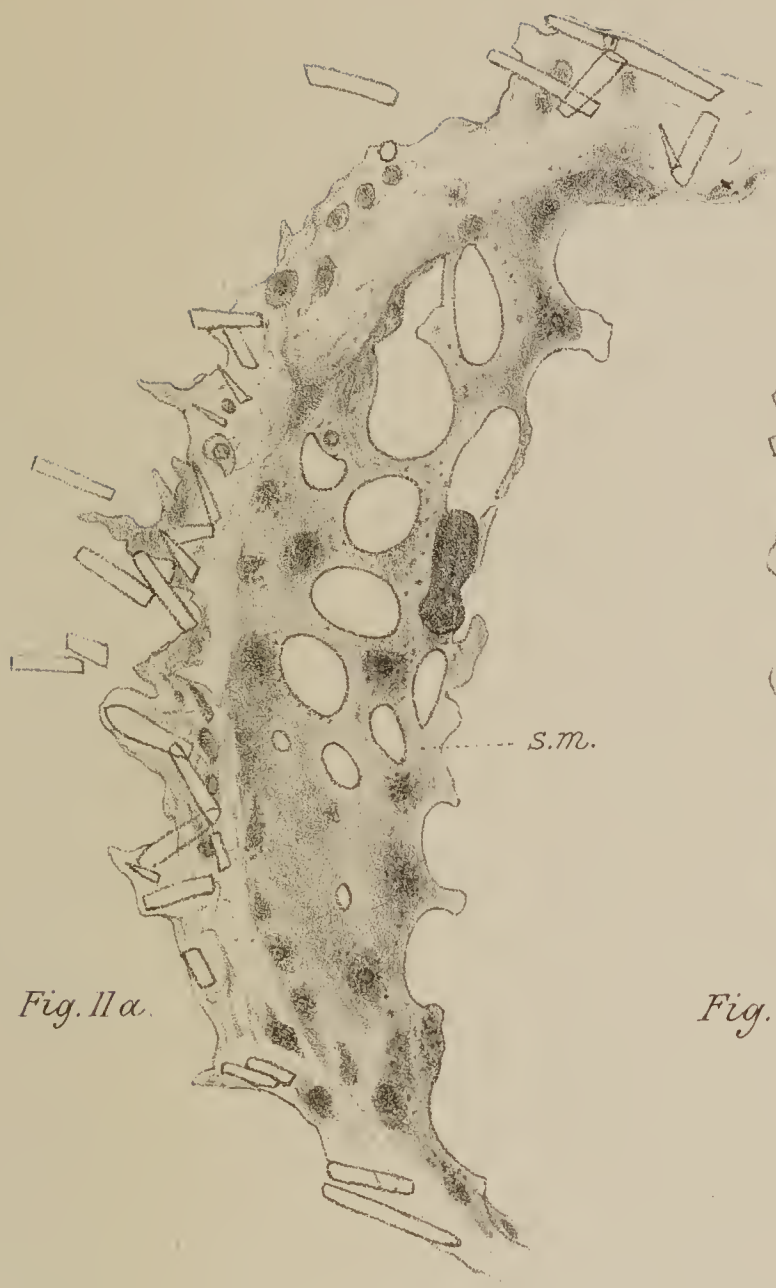
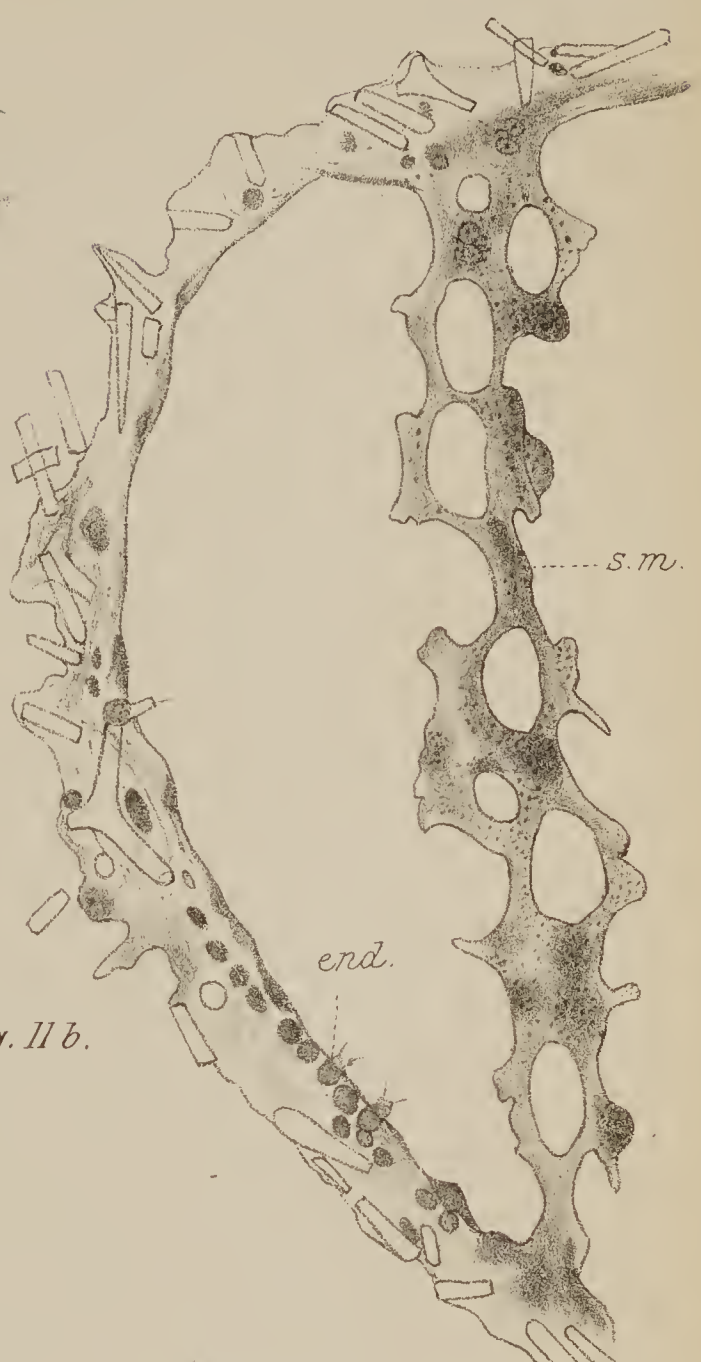


Fig. 11 a.



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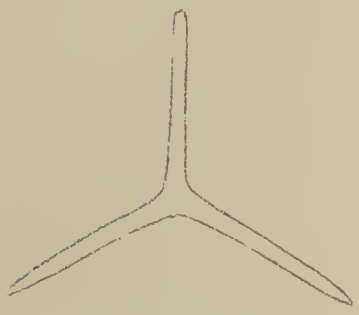

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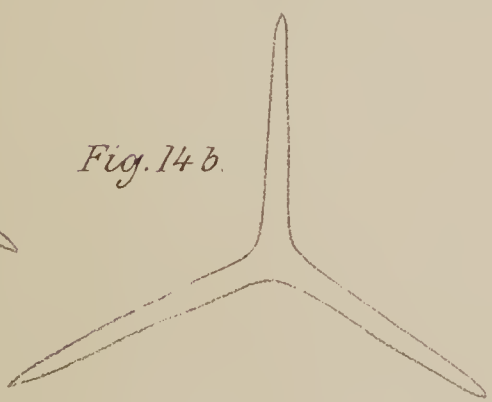

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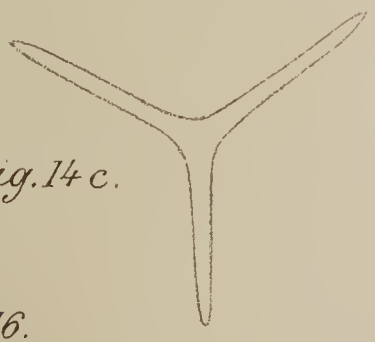

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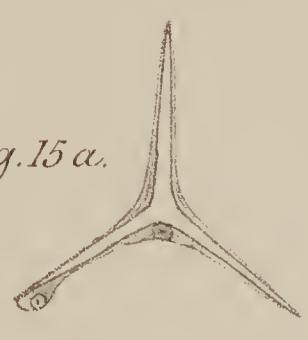

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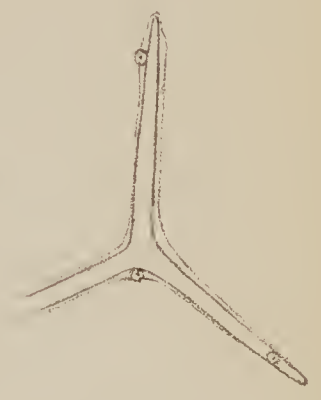

Fig. 15 b.

Fig. 20.

Fig. 19.

Fig. 21.

Fig. 16.

Fig. 17.

Fig. 18.

Fig. 22.

Notes on Two Acanthodriloid Earthworms from New Zealand.

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With Plates XV and XVI.

In the summer of last year (1890) I received, through the kindness of Professor Jeffrey Bell, of the British Museum, some earthworms for identification. They were collected by Mr. Vaughan Jennings in New Zealand, at Manngatua, south of Dunedin, who generously allowed me to retain them for further examination. I regret that so much delay has occurred in preparing my report for publication, for I almost completed my observations on them during last summer vacation, but continuous work since September last prevented me putting certain finishing touches to the descriptions and figures till August of the present year (1891).

I found in the bottle three worms and some fragments. One of these worms turns out to be Beddard's Neodrilus monocystis; the other two belong to a new genus.

Neodrilus monocystis, Beddard.

A single specimen[1] of a worm, found by Mr. Beddard amongst species of Acanthodrilus from New Zealand, differed from

[1] It is a curious thing that in so many cases only one specimen of a worm is found, which serves as a type of a new genus; and it has occurred to me, sometimes, that some of these may be hybrids or abnormalities, which from some weakness have failed to reach their burrows, just as we find the common earthworm on the surface of the ground after rains, &c., in a weakly or dying condition.

this genus mainly in the possession of only one pair of spermathecæ, and one pair of male pores (atriopores) on Segment XVII, instead of the usual two pairs of each of these structures. Beddard[1] himself appears to have had some doubts as to the generic value of these features, for he states that "it is possible that this supposed new genus Neodrilus is really an Acanthodrilus in which the posterior pair of male generative pores (atriopores), together with their glands, have not yet been developed." In my recent contribution in this Journal, "An Attempt to classify Earthworms," I placed Neodrilus as a "doubtful genus."

I am now, however, in a position to confirm and extend Mr. Beddard's brief description, although, like him, I had but one specimen, the anterior end of which after dissection I cut into a series of sections.

The general colour of the worm, in spirit, is sienna brown; its length about two and three quarter inches, with an average diameter of a quarter of an inch, but rather wider anteriorly to the clitellum. In shape it appears cylindrical, but is nearly square in transverse section, owing to the position of the four bundles of chætæ. There are 155 segments. The chætæ are in the usual four couples, which are equidistant, so that the outer couples lie on the dorsal surface (fig. 1). The clitellum, which is rather lighter in colour than the neighbouring region, occupies the Somites XIV to XIX. In addition, the dorsal surface of Somite XIII is also glandular, as is also the ventral surface of Somites XVIII and XIX where the glandular epidermis extends across the middle line.[2]

In Somite XVII, in a line with the ventral couple of chætæ on each side, is a conspicuous rounded papilla, the apex of which is distinctly lighter than the base. At the apex of each of these papillæ is the pore of the prostate (fig. 2, *prst. p.*).

On Somite XVIII, immediately behind those of Somite XVII, are two other papillæ, much less conspicuous and more depressed. These bear the apertures of the sperm-ducts. The

[1] 'Proc. Roy. Soc. Edinb.,' 1887, vol. xiv, p. 158.

[2] Beddard states that the clitellum occupies Somites XIII to XVII.

lips are tumid, and the pores are connected with those on Segment XVII by grooves (fig. 2).

Beddard describes much the same sort of arrangement, but states that the grooves from the pores on Somite XVII extend on to Somite XIX. I do not find this extension of the grooves backwards. The chætæ appear to be absent on Segments XVII and XVIII.

The prostomium is completely dovetailed into the buccal segment (fig. 1).

The most noticeable external feature, besides the position of the male pores, is the alternation of the nephridiopores (figs. 1 and 2), a fact which Beddard mentioned, and which is known in Acanthrodrilus dissimilis, and other species. This "alternation" is not quite regular, as will be seen from the following table, the pore being in front of sometimes the 4th, sometimes the 3rd or 2nd chæta, counting the most ventral chæta as the 1st:

Somite.			Left side.	Right side.
II.	Nephridiopore in front of	. .	4th chæta . .	4th chæta.
III.	„	„	. . 3rd „ . .	Worm injured.
IV.	„	„	. . 3rd „ . .	injured.
V.	„	„	. . 3rd „ . .	3rd chæta.
VI.	„	„	. . 3rd „ . .	3rd „
VII.	„	„	. . 3rd „ . .	2nd „
VIII.	„	„	. . 2nd „ . .	?
IX.	„	„	. . 2nd „ . .	2nd „
X.	„	„	. . 3rd „ . .	3rd „
XI.	„	„	. . ? „ . .	2nd „
XII.	„	„	. . 3rd „ . .	3rd „
XIII.	„	„	. . 2nd „ . .	2nd „
XIV.	„	„	. . 3rd „ . .	3rd „

And so on in regular alternation. A similar alternation in the position of the nephridiopores exists in the new genus described below.

Internal Anatomy.

There are no specially strong septa (fig. 3). The pharynx is covered by masses of glandular cells, as in the common earthworm, and resembling those which I described and figured

in Eminodrilus.[1] The gizzard lies in Somite VI. There are no calciferous glands, no typhlosole, nor intestinal cæca. The tubular intestine is slightly dilated in Somites VII, VIII, and enters the sacculated intestine in Somite XV.

Lateral hearts occur in Somites XI, XII, XIII, XIV, the first three being moniliform.

In accordance with the variations in positions of their pores, the nephridia lie latero-ventrally or latero-dorsally (figs. 4, 5), and exhibit slight differences in the mode of convolution of the tube and in other points. The inner (ventral) nephridium has a large cæcal portion to the bladder directed dorsally, while that of the dorsal nephridium is but feebly developed, the nephridiopore being placed near the end of the bladder (fig. 5). There is no nephridial network nor communication between the nephridia.

The Genital System.

The testes and ovaries have the usual position. There are three pairs of sperm-sacs in Somites X, XI, XII, that of the left side in Somite XII being much smaller than the right one (fig. 3).

The prostates are enormous, and there is but one pair of them. Each consists of two parts (figs. 3 and 6),—a soft, more or less cylindrical portion, which is white, glandular, constricted, and convoluted (*prst.*); and a short, narrow, shining duct (*pe. d.*). The latter opens externally in Somite XVII, and passes backwards into Somite XIX, where it joins the glandular region; this passes still further back to the 24th somite, and then bends forwards on itself, its free end (*a*) lying in Somite XVII, at the side of the duct.[2]

Lying above the prostate is a sac containing a bundle of penial chætæ (*pe. s.*) nearly as long as the prostate—that is about a quarter of an inch (figs. 6, 7). This penial sac opens

[1] "Report on an Earthworm from Equatorial Africa," 'Journ. Roy. Micr. Soc.,' 1891, Pl. IV, fig. 12.

[2] The shading in fig. 3 does not indicate satisfactorily the convolutions of the prostate.

externally on Somite XVII (fig. 8), by a separate pore from that of the prostate duct. Its wall is muscular, and its posterior extremity appears to be fixed to the body-wall by muscles. The sac contains four long, delicate penial chætæ, of which two are much longer than the others (fig. 9). The longer chætæ are sharply bent near their free ends, and this bent part is gracefully curved to a very fine point (fig. 9, *b*.). The shorter chætæ are not bent. The ends of all the chætæ are beset by numerous minute spines or asperities (fig. 10), and there appears to be a groove along one side, so that they are somewhat triangular in section.

When the prostate is removed or turned aside the sperm-duct can be traced along the body-wall to its pore in Somite XVIII (fig. 7). There is no trace of a prostate in Segment XIX.

The microscopic structure of the prostate is similar to that in Acanthodrilus, Deinodrilus, and other genera. The wall is formed of pyriform "clitellar" cells, amongst which a few blood-vessels occur. The whole is surrounded by a flat cœlomic epithelium (fig. 11, *a*). The penial duct is lined by short columnar cells, surrounded by a very thick muscular coat (fig. 12), around which are blood-vessels and cœlomic epithelium.

There is only one pair of spermathecæ in Somite VIII; at first sight, however, there appears to be two pairs of these organs (fig. 3); but the structures lying in Somite VII are in reality the appendices or diverticula of the spermathecæ, so common amongst earthworms. Mr. Beddard has already remarked upon the large size of the diverticulum in this species. On one side it is actually larger than the body of the spermatheca itself.

The spermatheca (fig. 13, *s*) is ovoid, with rather a thick wall, as can be seen in the left sac in fig. 3, where its dorsal wall has been removed. The sac communicates with the exterior by a short, thick, muscular duct, which resembles in its structure that of the prostate. This duct opens in the anterior region of the segment, and is joined close to the body-wall by the diverticulum. This is a sac of smaller or larger size than the main sac, roughly cylindrical and truncated, and contains spermatozoa.

Such is the coarse anatomy of Neodrilus monocystis; and though I have done little more than confirm Mr. Beddard, I have thought it worth while to illustrate its anatomy.

The present specimen was found by Mr. Jennings among "rotten wood and mould."

Plagiochæta punctata, n. gen., n. sp.

The other worms have a very distinctive shape and colouring, and have numerous chætæ arranged in a nearly complete circle.[1] The generic name[2] refers to the fact that the chætæ are always seen crossing the body, whether this is looked at above, below, or laterally. At a first glance, indeed, one might mistake them for species of Perichæta (or Megascolex); but the possession of two pairs of tubular prostates, amongst other anatomical characters, removes them from that genus.

Of this worm there were two complete and mature (?) specimens, and two halves of a third, but immature, worm.

The size and shape of the worm are rather characteristic (fig. 14); it is 1·6 inches long by 0·5 inch across its widest part, which is posterior to the clitellum, so that it is, compared to its length, very broad; it is composed of eighty-nine segments.

As will be seen from the sketch, which is twice the size of a spirit specimen, the anterior and posterior extremities are nearly similar, tapering gradually to the mouth and anus respectively. The clitellum forms, so to speak, a waist; but that it is in life narrower than the neighbouring anterior and posterior regions is, I think, doubtful.

The body is depressed, so that the dorso-ventral diameter is only about half the lateral breadth (Pl. XVI, fig. 17). A groove runs along the dorsal and ventral mid-line, which is probably due to shrinkage.

The general colour reminds one somewhat of Michaelsen's

[1] This suggested the name Cyclochæta for the genus, but Mr. Hatchett Jackson has employed the term for a genus of ciliate Protozoa.

[2] 'Jahrb. d. Hamburg wissensch. Anstalten,' vi, 1889.

Acanthodrilus (Mandane) pictus,[1] but is a richer chocolate-brown, with rows of white spots[2] (hence the specific name), which are more noticeable dorsally than ventrally.

A narrow dark band (fig. 14), due to absence of spots, extends along the whole length of the body in the middle line dorsally and ventrally, but becomes rather less marked towards the hinder end of the worm, and less noticeable ventrally. This dark band occupies the groove above mentioned.

The spots, which, though white in the spirit specimens, are perhaps only "light" in life, are very regularly arranged, forming transverse and longitudinal rows; and in each spot is embedded a couple of chætæ (Pl. XVI, fig. 18). On the majority of segments there are twenty-five to twenty-seven of these white spots, diminishing in the anterior segments to fifteen.

The median unspotted grooves are about three times as wide as the distance between any two white spots of a circle. At the hinder end of the body, for about a quarter of the total length of the animal, the spots are much closer together, giving the appear ance of a series of white rings. The ventral surface is much lighter than the dorsal and lateral surfaces, and the spots less noticeable.

The clitellum, though apparently not quite fully developed, is perfectly distinct; it occupies Somites XIV to XVII and part of XVIII. It is lighter in colour than the rest of the body, both dorsally and ventrally; and the white spots are quite distinct dorsally. As already mentioned, the body in the clitellar region is rather constricted.

The chætæ are numerous in each segment; they occur always in couples, each couple being embedded in a white spot (fig. 18). There are usually fifty to fifty-four chætæ in each somite, i. e. twenty-five to twenty-seven couples. They decrease in number in the more anterior somites, being forty-

[1] Πλαγιος, transverse.

[2] In a letter to me Mr. Jennings states that "while living they are lighter in colour than ordinary earthworms, and have a peculiar surface marking. Except contraction, they seem to undergo little change in spirit."

eight in Somite IV, forty-four in Somite III, and thirty in Somite II.

The chætæ are simple and sigmoid, without markings, and each is ·036 mm. in length.

The prostomium is completely dovetailed (fig. 15) into Somite I. I can find no dorsal pores.

The pores of the two pairs of spermathecæ are fairly large, and provided with white lips. Each pair lies in a median ventral depression, which is situated on the anterior margin of Somite VIII and of Somite IX; each pore being in line with the ventralmost couple of chætæ (Pl. XVI, fig. 16, *spth.*).

The spermiducal pores are not to be seen externally, but by means of sections I find them situated in Somite XVIII, in front of the ventralmost couple of chætæ.

There is an oval depression on the ventral surface of Somites XVII, XVIII, and XIX, bounded laterally by a distinct ridge. Within this depression, on each of the Somites XVII and XIX, is a pair of small transverse slit-like pores—those of the prostates—which lie in a line with the other genital pores (fig. 16, *prst.*).

The chætæ of these two segments appear to be absent, but in reality they are especially long, and are retracted into the body-cavity—in fact, have become modified for copulatory purposes.

The oviducal pores have the usual position on Segment XIV, though they are not visible externally.

The nephridiopores (*ne. o.*) are very distinct, even on the clitellum; they appear as light spots, which are larger than those around the couples of chætæ. These pores alternate in position (fig. 16), as in Neodrilus, &c.; this alternation being nearly but not quite regular, and sometimes not symmetrical. In the following table the position of these pores in regard to the chætiferous spots is shown. The first spot is the ventralmost, so that the fourth spot is latero-ventral (fig. 17^{4}), the tenth is latero-dorsal—in fact, lies on the dorsal surface, and is the fourth spot from the mid-dorsal line (fig. 17^{10}).

Specimen A.

No. of Somite.			Right side.	Left side.
III.	Nephridiopore in front of	. .	10th spot . .	10th spot.
IV.	„	„ . .	10th „ . .	10th „
V.	„	„ . .	5th „ . .	10th „
VI.	„	„ . .	5th „ . .	10th „
VII.	„	„ . .	4th „ . .	10th „
VIII.	„	„ . .	10th „ . .	4th „
IX.	„	„ . .	11th „ . .	10th „
X.	„	„ . .	4th „ . .	4th „
XI.	„	„ . .	10th „ . .	10th „
XII.	„	„ . .	4th „ . .	4th „

And so on, in a regular way, with a few exceptions, i. e. on the even-numbered somites the nephridiopores are dorsal, on the odd-numbered they are ventral till the twenty-third somite, when there are the following divergences from the rule.

No. of Somite.			Right side.	Left side.
XXIII.	Nephridiopore in front of	. .	10th spot . .	9th spot.
XXVIII.	„	„ . .	5th „ . .	4th „
XXX.	„	„ . .	4th „ . .	4th „
XXXI.	„	„ . .	9th „ . .	4th „
XXXII.	„	„ . .	5th „ . .	4th „
XXXIV.	„	„ . .	5th „ . .	4th „
XXXVI.	„	„ . .	5th „ . .	4th „
XXXVIII.	„	„ . .	5th „ . .	4th „
XL.	„	„ . .	5th „ . .	4th „
XLIII.	„	„ . .	10th „ . .	9th „
XLIV.	„	„ . .	5th „ . .	4th „
LIV.	„	„ . .	5th „ . .	4th „
LIX & LX.	„	„ . .	9th „ . .	9th „

In Specimen B.

No. of Somite.			Right.		Left.
III, IV, & V.	Nephridiopore in line with		10th spot	. .	10th spot.
VI.	,,	,,	9th ,,	. .	9th ,,
VII.	,,	,,	10th ,,	. .	10th ,,
VIII.	,,	,,	4th ,,	. .	4th ,,
IX.	,,	,,	9th ,,	. .	4th ,,
X.	,,	,,	4th ,,	. .	4th ,,
XI.	,,	,,	10th ,,	. .	4th ,,
XII. } XIV, &c. }	,,	,,	10th ,,	. .	10th ,,
XIII.	,,	,,	9th ,,		
XV. } XVII, &c. }	,,	,,	10th ,,		

In this specimen the variations from the normal position are fewer in the posterior region of the body than in specimen A.

The distances between the pores when normally situated are equal; that is to say, the space between right dorsal and left dorsal pores = space between dorsal and ventral pores = space between right ventral and left ventral pores. See fig. 17, where the position of the couples of chætæ are indicated by numerals.

It is so very generally taken for granted that the nephridiopores in any genus or species have a fixed relation to one of the couple of chætæ, that it is worth while to carefully note such deviations from the rule, as exhibited in this table, and in that for Neodrilus, and to bear in mind that even in Lumbricus and Allolotophora this pore is not invariably situated anteriorly to the ventral couple of chætæ. Claparède and Hering pointed this out some years back, and Borelli, in 1887, recurred to the matter,[1] and examined some half dozen of the common species of the family Lumbricidæ (*s. s.*) from this point of view. His results, which are not very detailed, show, however, that in some species, L. herculeus, for instance, nearly as many nephridiopores have not the "normal" position as have. In L. rubellus there are more

[1] 'Boll. d. Mus. Zool. ed Anat. Comp. Torino.,' vol. ii, No. 27.

pores in an "abnormal" position than in the normal, i. e. in front of the ventral chætæ. The "abnormal" position is itself variable, the pore sometimes occurring in front of the dorsal chætæ, sometimes dorsal of these, and even near the mid-dorsal line. Borelli does not state whether there is any approach to an "alternation," or whether the variability is more marked posteriorly than anteriorly.

There is little doubt that this sort of irregularity is of more frequent occurrence in other genera than we are apt to think. We have, amongst recorded cases (besides Plutellus), Beddard's description of Acanthodrilus dissimilis[1] and Ac. rosæ,[2] &c., where the alternation is not regular; Bourne's Perionyx saltans,[3] where there are two rows of nephridiopores, usually regularly alternating, though he mentions certain variations; Fletcher's[4] "Cupptodrilus" mediterreus, with an irregular alternation, and Megascolides tasmanicus, where the pores are in a sinuous series.

The deviation from any fixed positions is especially interesting in these genera, such as Acanthodrilus, Megascolides, and Cryptodrilus, in which some species are in a plectonephric condition, for it seems to support the theory of Beddard and Baldwin Spencer that this condition is primitive, and that the network communicated with extensively many scattered pores, as in Perichæta, &c.; when the meganephric condition supervened, by aggregation and enlargement of some portion of the network, the pores enlarged, and the nephridia now opened, not at some fixed point, as has usually been presumed to be the case, but at any point on the surface of the segment, the relatively fixed portions being probably a later phenomenon, and its relation to the bundles of chætæ being due to some secondary causes, with which at present we are unacquainted.

[1] 'Proc. Zool. Soc.,' 1885, p. 822.
[2] This Journal, vol. xxx, p. 434.
[3] 'Proc. Zool. Soc.,' 1886.
[4] 'Proc. Linn. Soc.,' N.S.W., 1887, p. 601.

INTERNAL ANATOMY, Pl. XVI, fig. 19.

There are no especially strong septa (though those of XIII/XIV, XIV/XV, and XV/XVI are slightly thicker than the rest), nor any great displacement of organs.

The Alimentary Canal.—The pharynx, which occupies the Somites III, IV, and part of V, is partially concealed by two pairs of lobulated masses, or "salivary glands" (*Sal.*), lying dorsally and laterally in Somites IV and V, the gland in the latter being bilobed. These are not modified nephridia, but consist of groups of large granular cells, deeply stained in borax carmine, and closely resembling the "salivary glands" of Eminodrilus,[1] &c.

The pharynx is internally divisible into a ventral cuticulated region, and a dorsally placed flattened diverticulum, laterally produced, and lined by tall ciliated cells, as in many other, perhaps all earthworms.

The œsophagus, which is not ciliated, is narrow and tubular: it passes backwards to the large sacculated intestine, which commences in Somite XVI.

The hinder region of the œsophagus in Somites X to XIII is highly vascular, and its wall thrown into folds; these become more definite in Somite XIV and give rise to a well-marked pair of calciferous glands. Each is a large sac, laterally placed, but extending dorsally and ventrally, so that the pair almost surround the œsophagus (Pl. XVI, fig. 20, *cal.*). Its structure calls for no remark.

There is no gizzard to be detected on dissection, but in Somite VI the wall of the gut is slightly more muscular than elsewhere, the coat being about twice the thickness of that of the neighbouring tract, instead of eight to ten times as thick, as in the case of the functional gizzard in most earthworms. The sacculated intestine commences in Somite XVI, where it suddenly dilates, to become about three times the width of the œsophagus. This character it retains in Somites XVII, XVIII, and XIX, beyond which it is spirally coiled (Pl. XVI, figs. 19, 21). This condition has been described in Didy-

[1] Benham, 'Journ. R. Micr. Soc.,' 1891, pl. iv, fig. 12.

mogaster by Fletcher;[1] and when I first examined the present worm I believed that the spiral appearance was merely due to contraction, causing the gut to bulge, first on one side and then on the other. But it is a true spiral, as can be seen by dividing the worm either longitudinally or transversely (Pl. XVI, figs. 17, 21). There is no typhlosole, nor are there any cæca, such as are found in most species of Perichæta.

The nephridia are large, conspicuous (Pl. XVI, fig. 19), and alternate in position in correspondence with the position of the nephridiopores; the funnels, however, are always placed below the gut, and in line; they do not share in the alternation. The nephridium (Pl. XVI, fig. 22) presents the usual regions described by me for Lumbricus and other genera;[2] the coils are arranged somewhat differently in the dorsal and ventral series, and there is a dilated cæcal bladder, which is longer in the dorsal nephridia than in those of the ventral series.

The funnel has the same general structure as in Perichæta malamaniensis—that is to say, there are no centripetal marginal cells; but whereas in that species all the eight cells are of the same size, in the present worm there is a difference in size, and an increase in number of the marginals, as in P. aspergillum. I append two figures (fig. 23, *a*, *b*) representing two consecutive sections through a funnel; and from it there appears to be about sixteen marginals, which decrease in size on each side of the funnel. I am doubtful as to the presence here of a "central cell,"[2] and can readily believe that this is absent, as is the case in some Perichæta.

The first full-sized nephridium in the second segment is in Somite III; but there is a pair of rudimentary structures which are, I believe, degenerate nephridia.

That on the left is a fairly typical though very small nephridium; the one on the right is much less developed.

This very minute organ only occupies some four or five

[1] 'Proc. Linn. Soc.,' N.S.W., 1886.

[2] This Journal, vol. xxxii, p. 293.

sections in a longitudinal series; these are represented in Pl. XVI, fig. 24, *a*, *b*, *c*, *d*.

A small pore on the anterior margin of Somite 11, just outside the peripharyngeal nerve commissure, leads by a short duct with a narrow lumen into a dilated portion (fig. 24, *b*.), which is filled with a coagulum (*coag*.); from this "bladder" a tract of cells (fig. 24, *c*.) leads backwards to a small coiled tubule which appears to end blindly (fig. 24, *d*.). I am unable to detect a lumen in the tract of cells lying between this coil and the "bladder."

On the opposite side of the body, occupying the same position as this minute structure, which is absent on this side, I find the small nephridium above mentioned; so that I think there can be little doubt as to the correctness of my interpretation of this minute organ as a "vestigial" nephridium. I expected that these two small nephridial pores and ducts would lead to "peptonephridia," but such is not the case; there is no modification of the anterior nephridia other than degeneration.

Genital System.

The two pairs of testes, and of spermiducal funnels, the pair of ovaries and oviducts, are placed in the usual segments. The ovary (Pl. XVI, fig. 25) is rather remarkable, in that the ripe ova are not confined to the tip of the organ, but are present along the whole of one side. The ovary is attached to the septum by only a small peduncle; it is not pear-shaped, as in Lumbricus, but slightly lobed, and more closely resembling the testes in shape than is usually the case. I am not acquainted with any ovary amongst the Oligochæta with exactly this form, though Horst has figured some curiously shaped ones in Benhamia Schegelii,[1] where it is rosette-shaped; B. Buttikiferi,[2] where it is somewhat like the parent ovary. The oviducts open close to ventralmost chætæ of their respective sides, at the tip of very slight papillæ.

[1] 'Notes from the Leyden Museum,' 1887, pl. iv, fig. 7.

[2] Ditto, pl. v, fig. 6.

There are four pairs of lateral sperm-sacs (fig. 19, *sps.*), almost filling the Somites IX, X, XI, and XII, and hiding the œsophagus and the two median sperm-sacs which lie below the gut in Somites X, XI, and enclose the testes and ciliated rosettes.

There are two pairs of prostates, in Somites XVII and XIX respectively. Each prostate (figs. 19 and 26, *pro.*) is a soft, irregular body, but roughly cylindrical, terminating in a free, blunt point, placed dorsally. The free end is sharply curled upon itself; the prostate then gradually widens, and is slightly convoluted as it passes downwards at the side of the intestine towards the ventral wall of the body, just before reaching which its character suddenly changes, both in appearance and in structure. This "penial duct" (fig. 26), as I will call it, is much narrower than the glandular part or prostate, and is slightly curved as it penetrates the body-wall to open by the pores seen externally. In appearance, instead of the dull, whitish, uneven character presented by the prostate, the penial duct is smooth and glistening, due to the fairly thick layer of circular muscles which forms its wall (fig. 28). The histological structure of the prostate is similar to that of Neodrilus. In fact, these prostates are closely similar to those of Acanthodrilus and its allies, but are less compact in appearance.

In front of each prostate is a sac containing long penial chætæ (figs. 26, 29). Each sac enters the body-wall immediately in front of the penial duct, but, as can be seen in section (Pl. XVI, fig. 29), crosses the duct in the thickness of the body-wall, and opens independently to the exterior just behind, and rather to the outer side of it. Each sac is in reality double, and each subdivision contains a couple of chætæ, of which one is small (*b*) and no doubt in reserve, the other being longer (*a*). There appears to be no particular marking or other peculiarity about these penial chætæ. The ordinary chetæ are absent in these somites, and the penial chætus occupy their places, as is usually the case in Acanthodrilidæ.

There are two pairs of spermathecæ (figs. 19, 30), each consisting of two parts, as is so generally the case in the

prostatiferous worms, viz. (1) a subglobular sac with a short, thick, muscular duct opening externally on the anterior edge of the segment; and (2) a conspicuous, curved, cylindrical, glistening diverticulum or appendix, which lies in the segment in front of that containing the main sac, with the neck of which it communicates. The spermathecæ lie in Somites VIII and IX, so that the appendices are in Somites VII and VIII respectively.

Repeated observations have shown that in spermathecæ formed on this plan the sac does not contain spermatozoa, which are, as Beddard was the first to point out, found only in the diverticulum. This is, on the whole, true in this case too, although in sections through the organs I detected a few spermatozoa in the neck of one of the spermathecæ (Pl. XVI, fig. 31).

The microscopic structure of the spermatheca is illustrated by figs. 31 and 32. The former, which is combined from two or three of a series of longitudinal sections, represents the general relation of sac to appendix, and the position of the cells which are shown enlarged in fig. 32. The lining cells of the sac itself are very much taller than those of the appendix, and of slightly different structure when fully developed.

The appendix has, outside the epithelium, a thick muscular coat (*mus.*). This is absent in the wall of sac, except around the neck. The muscle fibres are continuous with the circular coat (*c. mus.*) of the body-wall, which is here very strongly developed.

The cavity of the sac contains some granular matter (*x*), which is produced by the epithelial cells (fig. 32 *b*), together with a few spermatozoa (*spoa.*). Each cell is columnar, with an oval nucleus near its inner end. The rest of the cell is occupied by a finely spherular or granular secretion (*x*). It appears that when the cells have reached a maximum of activity the free end projects into the lumen of the sac and discharges its contents, leaving then a vacuole or space near this free end (as at *m.*). It then probably shrinks, and gradually elongates again as renewed activity commences. The nucleus is only

feebly stained, and the contents of the cell remain unstained in borax carmine.

The epithelium of the appendix (figs. 31 and 32 *c*) consists of tall columnar cells, not quite so high as those of the sac. The outer free end of each cell is flat, and the inner end of all the cells in my sections is bent at a slight angle to the body of the cells, and at this point lies the nucleus. This is smaller than that in the epithelium of the sac, and stains much more deeply: it is surrounded by a deepy staining almost homogeneous protoplasm. The rest of the cell is occupied by similar granules to those found in the epithelial cells of the sac.

The appendix is filled with spermatozoa, which are to some extent regularly arranged, with the heads towards the walls, and the tails directed centrally. The heads appear embedded in or attached to the epithelium (figs. 31, 32, *d*). The cells in these regions are much shorter, less than half the length of those just described; and have no definite outer surface: otherwise they resemble the above-mentioned cells. Intermediate conditions between *c* and *d* can be seen in the sections.

It is probable that the cells of the appendix do not simply discharge their product, but disintegrate, leaving only the nucleus and homogeneous protoplasm behind, which will come into renewed activity, and give rise to more secretion during the next breeding season.

The spermatozoa, as seen in the section, are arranged as if they formed a sperm-rope, but the heads and tails are reversed when compared with sperm-rope of Tubificidæ, &c., which may perhaps be due to the fact that there would be no opportunity for the use of the tails for locomotion of the sperm-rope in earthworms.

We are totally ignorant of the purpose of this sperm-rope in earthworms, and it is a matter of some uncertainty as to where they are formed in Lumbricus, &c.; but it seems, from the above observations and others made by Beddard that, in those genera which have "an appendix" to the spermatheca, the sperm-ropes or spermatophores are formed in that portion of the organ.

Among the bases of these cells are a few roundish nuclei without any stained protoplasm. These perhaps help in the renewal of the epithelium.

The duct (at *a.*, fig. 31), common to the sac and the appendix, is lined by a layer containing two sorts of cells, the nuclei of which differ in shape, size, and capacity for stains, and in position in the cell. In sections two rows of nuclei are evident, a deeper and a more superficial series. The nuclei nearer the base of the epithelium are more deeply stained, and about half the length of those of the outer row, which themselves are so placed that their outer ends are at about the middle of the cells (see fig. 32 *a*). The latter, longer nuclei belong to narrow cells filled with granules similar to those in other parts of the spermatheca. The shorter nuclei, which alternate with and lie more deeply than the others, belong to clear cells without any very definite contents. The alternation of the cells is quite evident with a high power, and is very regular. The spaces between the granular cells are not artificial, as the figure might suggest, but are occupied by excessively fine protoplasmic (?) contents. These two sorts of cells are, no doubt, modifications of the ordinary columnar and goblet cells of the epidermis.

Locality.—These worms were found, with the specimen of Neodrilus, amongst mould and decaying wood at Manngatua, south of Dunedin.

Affinities of Plagiochæta.

This new genus apparently has affinities in two directions viz. with Perichæta and with Acanthodrilus. The circle of chætæ is known in Perionyx and Perichæta (including Megascolex and Beddard's sub-genera); but in no form do I find any mention of the chætæ being in couples, in the way in which they are arranged in the present genus. Again, the position of the genital pores marks it off from Perichæta, where both spermiducal and spermathecal pores are much further removed from the ventral mid-line than is here the case, while the male pores are usually on papillæ.

These pores in Perionyx are, relatively to the chætæ, in about the same position as in Plagiochæta, but the male pores and oviducal pores are in depressions.

The position of the clitellum and its appearance are more Perichætous than Acanthodriloid.

With Perichæta Stuarti it is in agreement in the position of the genital pores and in the character of the prostates; but this species has no appendix to its spermatheca, and differs from Plagiochæta in other points.

The alternation of the nephridiopores calls to mind Perionyx saltans of Bourne, Acanthodrilus novæ-zealandiæ, and other species, and Plutellus of Perrier; but with none of these does it agree in the essential generic characters.

The genus differs considerably in its internal anatomy from Perichæta, viz. in the character of the nephridium, in the shape of the prostates, in the position of these, and the possession of two pairs of them; in the presence of calciferous glands, in the absence of gizzard and of intestinal cæca; in the arrangement of sperm-sacs, in the shape of the ovary, &c.[1]

With Acanthodrilus it agrees in the position of the male pores and in the character of the prostates, and with some species in the arrangement of the nephridia, and in the presence of sacs containing penial chætæ. But Plagiochæta differs from Acanthodrilus, and its allies Trigaster, Benhamia, and Deinodrilus, in the form of the clitellum, in the arrangement of the chætæ, in the absence of a gizzard (cf., however, Ac. Georgianus, Mich.).

Mr. Beddard has pointed out that the interesting genus Deinodrilus presents a somewhat similar mixture of Perichætoid and Acanthodriloid characters; and it seems to me that Plagiochæta more closely resembles in certain points each of these genera. In its locomotor organs it is closely

[1] P. intermedia, Beddard, and P. Bakeri, Fletcher, however, possess two pairs of prostates, which are cylindrical or "acanthodriloid" in the former species.

connected apparently with Perichæta, while its genital and alimentary systems are on the Acanthodriloid plan.

The genus appears to support the view as to a Perichætous condition which I have put forward in my recent paper on the "Classification of Earthworms" (p. 275), viz. that it is not primitive, but secondary, and hence may be developed in any family.

It seems evident, too, that the meganephric and plectonephric condition may occur within the same genus, as we see to be the case in Acanthodrilus, and that this condition of the nephridium is not of itself sufficient to decide to which series of families a genus belongs. The sum of the characters of Plagiochæta places it amongst the Plectonephrica, mihi, or Acanthodrilini of Beddard.

The general features of its internal anatomy point to its close affinity with the family Acanthodrilidæ, mihi, rather than with the Perichætidæ.

Beddard forms two families, Deinodrilidæ and Acanthodrilidæ, to contain the genera which I have grouped in one family. I think that we shall do well to wait awhile before we subdivide the families too much; and I would still retain Deinodrilus in the same family as Acanthodrilus, Trigaster, and Benhamia, for it differs from these only in the possession of twelve chætæ; the extent of clitellum not being even a generic distinction, since it varies in different species of Acanthodrilus.

I therefore place Plagiochæta as a fifth genus in the family Acanthodrilidæ, mihi, with the following characters:— The chætæ are numerous, and arranged in couples, so as to form nearly a complete circle in each somite. The clitellum is short. There are four sperm-sacs; the spermathecæ have diverticula; penial chætæ replace the ventral chætæ of Somites XVII, XIX; a pair of calciferous glands is present. There are no peptonephridia; no dorsal pores. Some of these characters are shared by some one or more of the other genera of the family.

It is possible that Bourne's P. Stuarti may belong to this

family, but it is to be regretted that we have received no detailed account of the anatomy of this and the other interesting forms which have been briefly described by him.[1]

[1] 'Proc. Zool. Soc.,' 1886.

EXPLANATION OF PLATES XV and XVI,

Illustrating Mr. W. Blaxland Benham's "Notes on Two Acanthodriloid Earthworms from New Zealand."

Neodrilus monocystis.—Figs. 1 to 13.

Fig. 1.—Dorsal view of anterior end of body, showing the character of the prostomium (*pr.*), arrangement of chætæ (*d. ch.*), and position of the nephridiopores (*ne. o.*) in these somites.

Fig. 2.—Ventral view of the somites in the neighbourhood of the genital pores. *ne. o.* Nephridiopores. *prst. p.* Pore of the prostate. *sp. p.* Spermiducal pore. *v. ch.* Ventral chætæ.

Fig. 3.—General anatomy, as seen when the worm is opened in the usual way; from the dorsal surface. *app.* Appendix of spermatheca. *d. v.* Dorsal vessel. *giz.* Gizzard. *l. h.* One of the lateral hearts. *ne.* Nephridium. *pe. d.* Penial duct. *pe. s.* Sac with penial chætæ. *prst.* Prostate. *sp. s*^{1}. Anterior sperm-sac. *sp. s*^{3}. The most posterior (third) sperm-sac. *spth.* The main sac of the spermatheca.

Fig. 4.—A transverse section of the worm behind Somite xxx, showing the general squareness of the worm, the position of chætæ, and of the nephridia. It would be unusual to find the asymmetry of the last structures as represented in the figure. *a.* Separation of dorsal muscle bundle into two lateral halves. *b.* Lateral muscle bundle. *c.* Ventral muscle bundle. *d.* Accessory muscle bundle, separated from *c* by penetration of a nerve into the body-wall. *d. ch.* Dorsal chætæ. *d. n.* Dorsal nephridium. *d. v.* Dorsal blood-vessel. *m.* Band of muscle passing from the dorsal to the ventral bundle of chætæ, and acting as their retractor. *N.* Nerve-cord. *v. ch.* Ventral chætæ. *v. n.* Ventral nephridium. *v.* $'v$. Ventral blood-vessel.

Fig. 5.—The inner surface of body-wall (rather more than half the worm is represented), to show position of the nephridia in consecutive segments. Letters as in Fig. 4.

Fig. 6.—A portion of Fig. 3, more enlarged (× 8). It represents the prostate of the eighth side; the numbers are placed nearly in the mid-ventral line. *Prst.* Prostate. *a.* Its free extremity. *pe. d.* Penial duct. *pe. s.* Sac with penial chætæ.

Fig. 7.—The sac of the penial chætæ, which protrude from its cut end which is turned forwards, and the prostate are cut away to show the sperm-duct (*sp. d.*) entering the body-wall in Somite XVIII.

Fig. 8.—A diagrammatic longitudinal section through this region of the body-wall, to show the pores of the penial duct of the sac with penial chætæ, and of the sperm-duct. [It is compiled from a series of sections.] *ci.* Circular muscles of the body-wall. *ep.* Epidermis. *lg.* Longitudinal muscles of the body-wall. *pe. ch.* One penial chæta in the sac (*pe. s.*). *pe. d.* Penial duct opening to the exterior, independently of the sac of penial chætæ. *pores.* Aperture common to the prostate duct and penial sac. *Prst.* Prostate. *pr. pap.* Papilla carrying the pore of the prostate and penial sac. *sp. d.* Sperm-ducts. *sp. p.* Spermiducal pore. *v. ch.* Ventral chætæ.

Fig. 9.—The sac with penial chætæ; it was broken in removing it from the body, and the two portions *a* and *b* are really continuous at *x*.

Fig. 10.—A portion of one of the long penial chætæ, very highly magnified to show the notched ridges and the triangular section. It is surrounded by the cuticular membrane (*m.*) which lines the sac.

Fig. 11.—Transverse section through the prostate. *a* is the cœlomic epithelium surrounding it. *bv.* Blood-vessels in the wall. Only a few cells are represented in detail, the rest in outline.

Fig. 12.—Transverse section of the penial duct. *ep.* Its epithelium. *m.* Its muscular coat. *v.* Blood-vessels.

Fig. 13.—The spermatheca of the right side. *s.* The chief sac. *app.* The appendix or diverticulum. *d.* The duct penetrating the body-wall.

Plagiochæta punctata.—Figs. 14 to 32.

Fig. 14.—Dorsal view of the worm (× 2), to show the characteristic marking (from a spirit specimen). *cl.* Clitellum. *pr.* Prostomium.

Fig. 15.—Dorsal view of anterior end of worm, showing the shape of the prostomium.

Fig. 16.—Ventral view of the anterior 23 somites, showing the characteristic arrangement of the chætæ (represented by dots) in couples, the position of the nephridiopores (*ne. o.*), the pores of spermathecæ (*spth.*) in depressions, the prostate pores (*prst.*[1], *prst.*[2]) also in a depression. *clit.* Clitellum. *m.* Mouth. *pro.* Prostomium.

Fig. 17.—A transverse section of the worm behind the clitellum, showing the way in which the longitudinal muscular coat (*lg.*) of the body-wall is

broken up by the chætæ; these are not represeuted, but occur in couples at the spots marked with numerals; the position of the nephridia (*n. v.*, *n. d.*) is also shown. *D. v.* Dorsal blood-vessel. *Int.* Intestine, spirally coiled, a part of it showing through the septum (*sep.*). *N.* Nerve-cord.

Fig. 18.—About half of a segment (drawn to scale), showing the couples o chætæ inserted in light areas, the pigmented part being represented diagrammatically.

Fig. 19.—A general view of the internal anatomy, as seen when the dorsal portion of the body-wall is cut away. *app.* Appendix of the anterior spermatheca. *cal. gl.* Calciferous gland. *d. v.* Dorsal vessel. *int.* Intestine. *ne. ne.* Nephridia. *pro.*[1], *pro.*[2] The two prostates. *sal.* Salivary glands. *sp. s.*[1], *sp. s.*[4] The most anterior and most posteroir sperm-sacs. *spth.* The main sac of the spermatheca.

Fig. 20.—Transverse section of œsophagus and calciferous gland, represented diagrammatically.

Fig. 21.—A longitudinal section of the intestine, to show its spiral coils. *sep.* Septa.

Fig. 22.—One of the ventral nephridia (the funnel is not shown). *a.* The convoluted large and middle tubes. *b.* The coil of small tubes. [These are only represented diagrammatically; it is not intended to show the exact arrangement of *a*, *b*.] *c.* The cæcal portion of the bladder. *p.* Portion leading to the nephridioporc.

Fig. 23.—Two consecutive sections (*a*, *b*) through a nephridial funnel (from a series of transverse sections). *c. ep.* Cœlomic epithelium. *m.* Marginal cells.

Figs. 24, *a*, *b*, *c*, *d*.—Four consecutive sections through the degeneratc nephridium of the second segment. In *a* one edge of the nephridiopore and a part of the dilated bladder is seen. *b* goes through the nephridiopore. *coag.* Coagulum in bladder. *m.* Muscle. I, II. Portion of wall of the 1st and 2nd segments: *c* shows the tract of cells leading to the convoluted tube, a portion of which (*t*) is present. *m* is the position occupied in the next section by the coil *d*. *l* shows the position occupied by the tract of cells represented in *c*. *b. v.* Blood-vessels.

Fig. 25.—An ovary attached to septum (*spt.*).

Fig. 26.—View of the prostates, &c., after removal of the gut. *pe. s*[1]., *pe. s*[2]. The two sacs containing penial chætæ. *pro*[1]., *pro*[2]. The two prostates. *sp. d.* Sperm-duct. *pe. d.* Penial duct.

Fig. 27.—Transverse section of a sperm-duct, showing the oval nuclei with long axis at right angles to the axis of the duct. *b.* Blood-vessel.

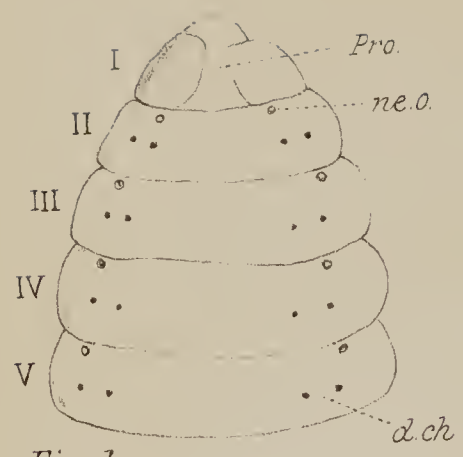
Fig. 28.—Transverse section of penial duct. Here the nuclei of the epithelium have their long axes radially placed. *c. m.* Circular muscular coat. *lg. m.* Longitudinal muscles.

Fig. 29.—Diagrammatic obliquely longitudinal section through the aperture of prostate, combined from a series of sections. *Pe. d.* Penial duct. *pr.p.* Prostate pore. *pe. s.* Sac with penial chætæ. *a.* The longer; *b*, the reserve penial chæta. *p. s. p.* Pore of this sac.

Fig. 30.—A spermatheca, showing its various parts.

Fig. 31.—A longitudinal section through a spermatheca (combined from a series of sections). *a, b, c, d* point to the regions which are represented more highly magnified in Fig. 32. *a.* The duct of spermatheca. *app.* The diverticulum. *b.* Wall of the sac. *c. m.* Circular muscle of the body-wall. *c. d* Epithelium of appendix. *lg. m.* Longitudinal muscle of the body-wall. *mus.* Muscular coat of the diverticulum. *sept.* Septum VIII/IX. *spoa.* Spermatozoa in the diverticulum, and a few in the sac. *v. ch.* Ventral chætæ. *x.* Granular secretion in the sac.

Fig. 32.—Portions of epithelium of the spermatheca from different regions. *a.* From duct. *g.* Glandular cells. *p.* Nuclei of non-glandular cells. *b.* From the wall of the sac. *m.* Cells which have probably just discharged their contents (*x*). *n.* Cells not quite fully developed. *c.* From the diverticulum. *k.* Nucleus of the interstitial cell. *d.* Also from the diverticulum, showing spermatozoa attached to the cells by (*h.*) their heads. *t.* Tails of spermatozoa.



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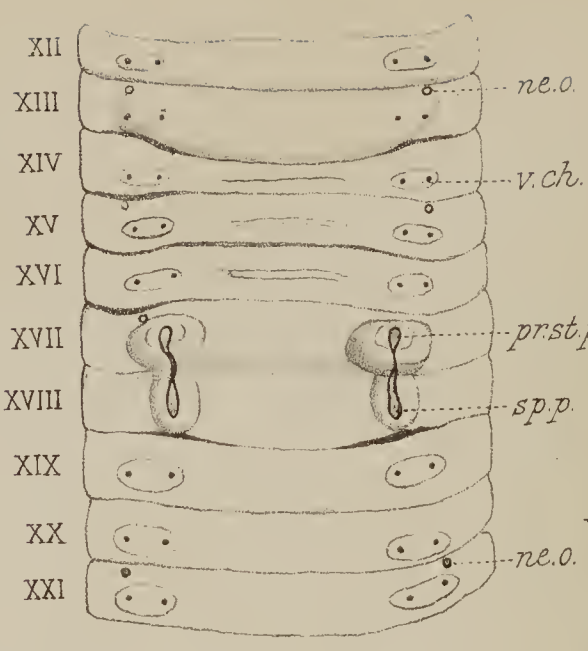

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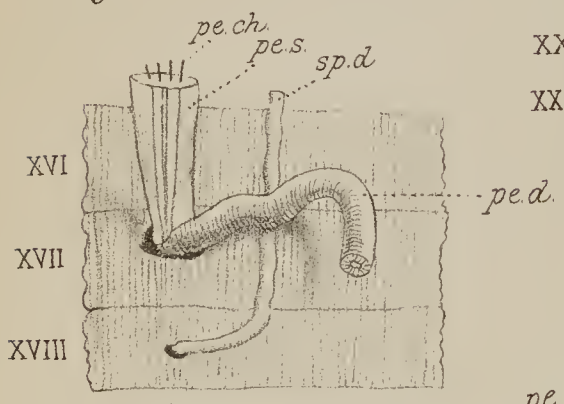

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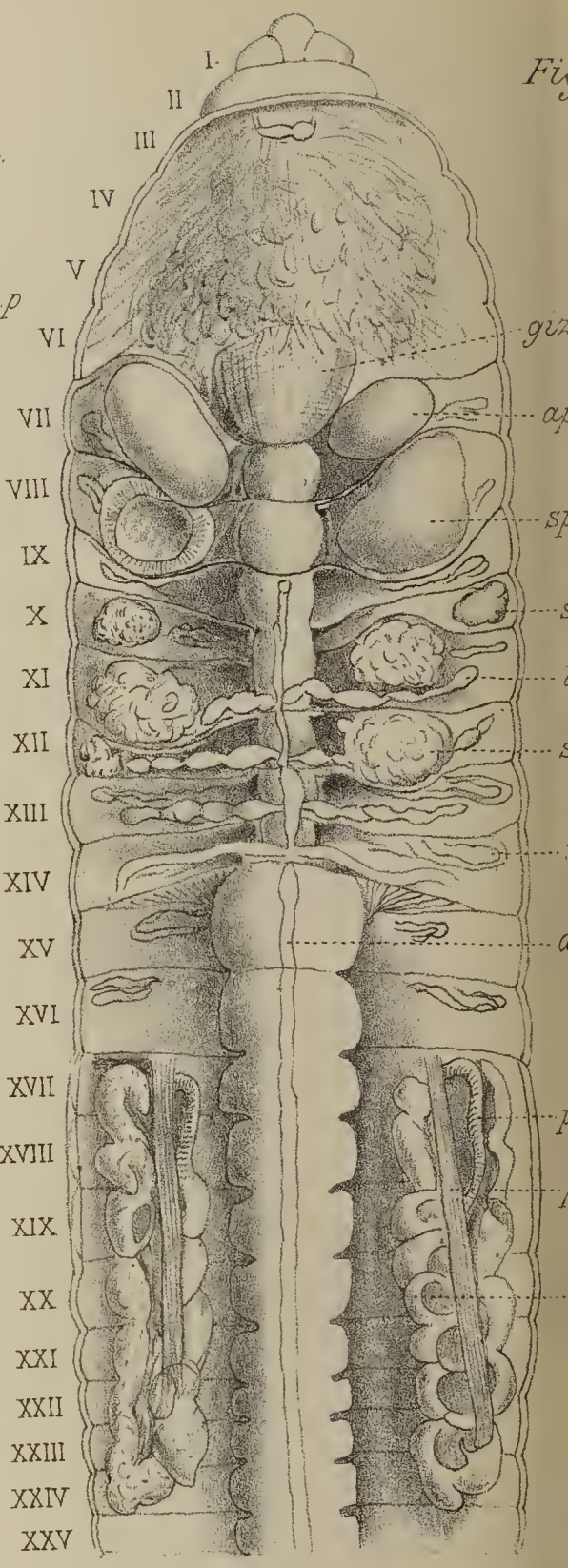

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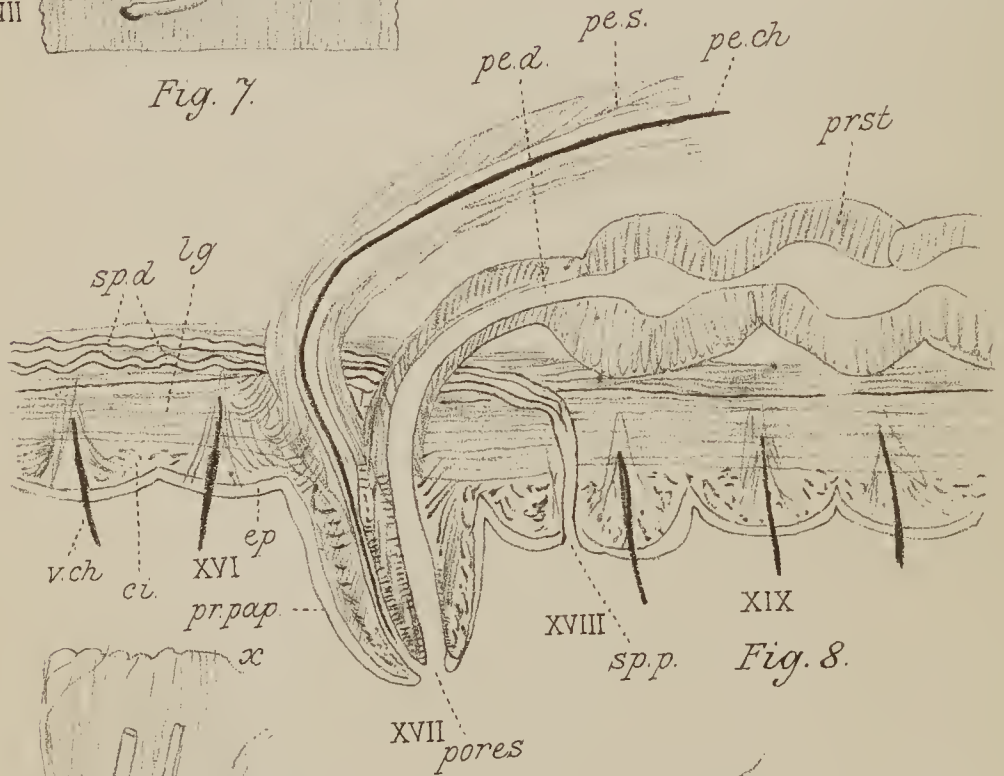

Fig. 8.

Fig. 9.

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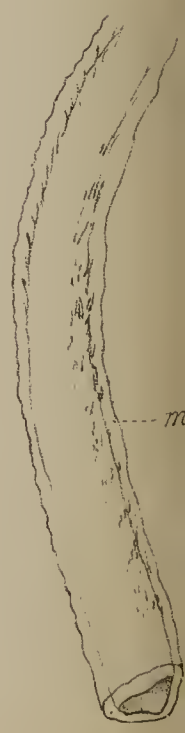
Fig. 11.



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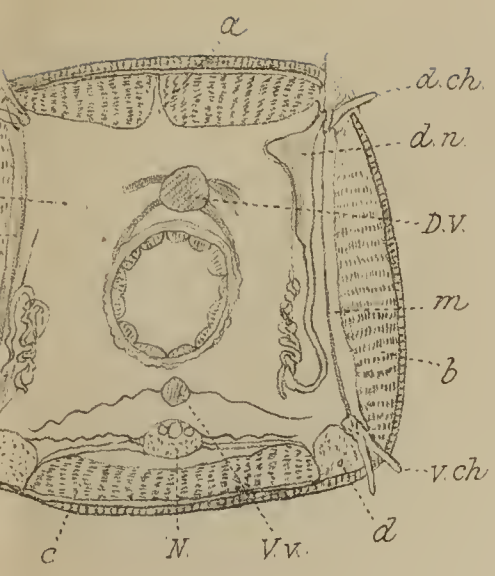

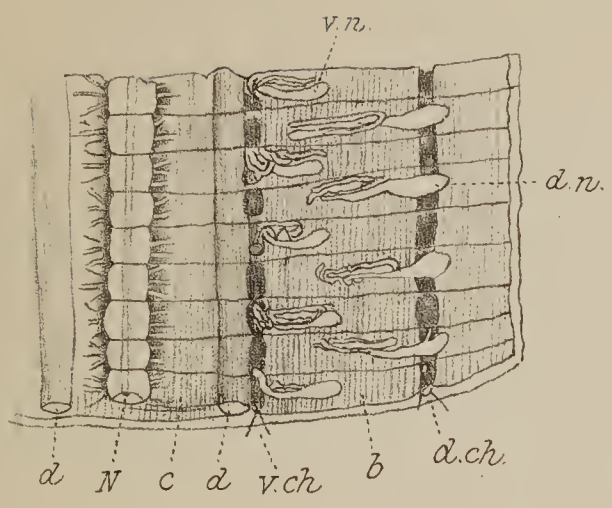

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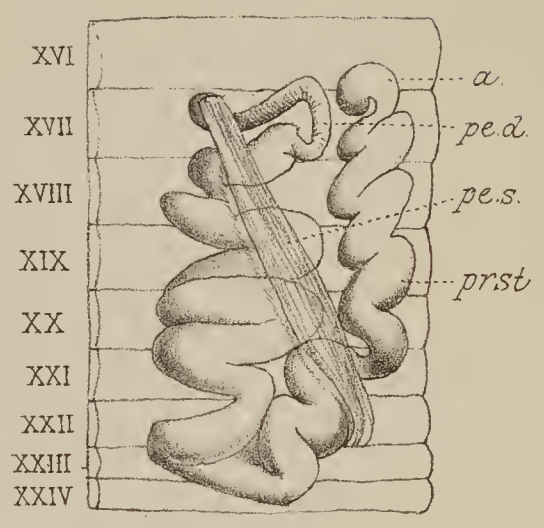

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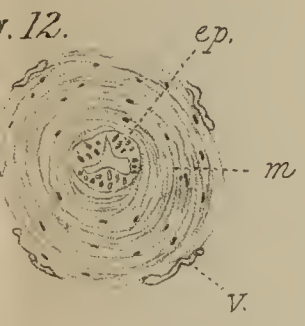

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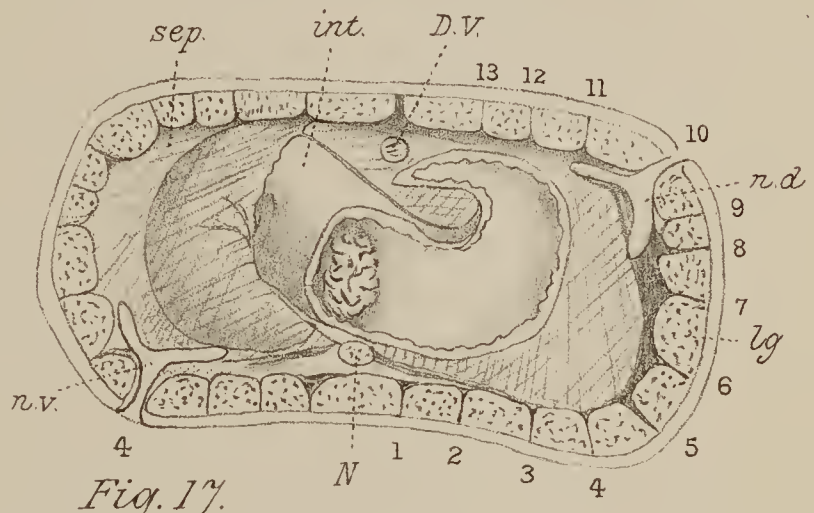

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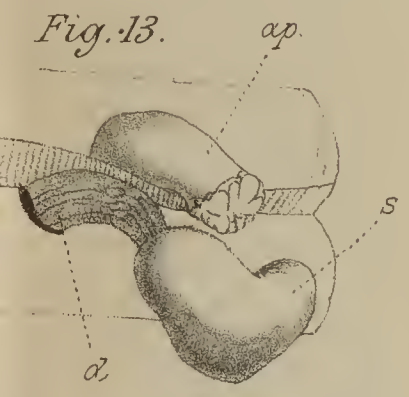

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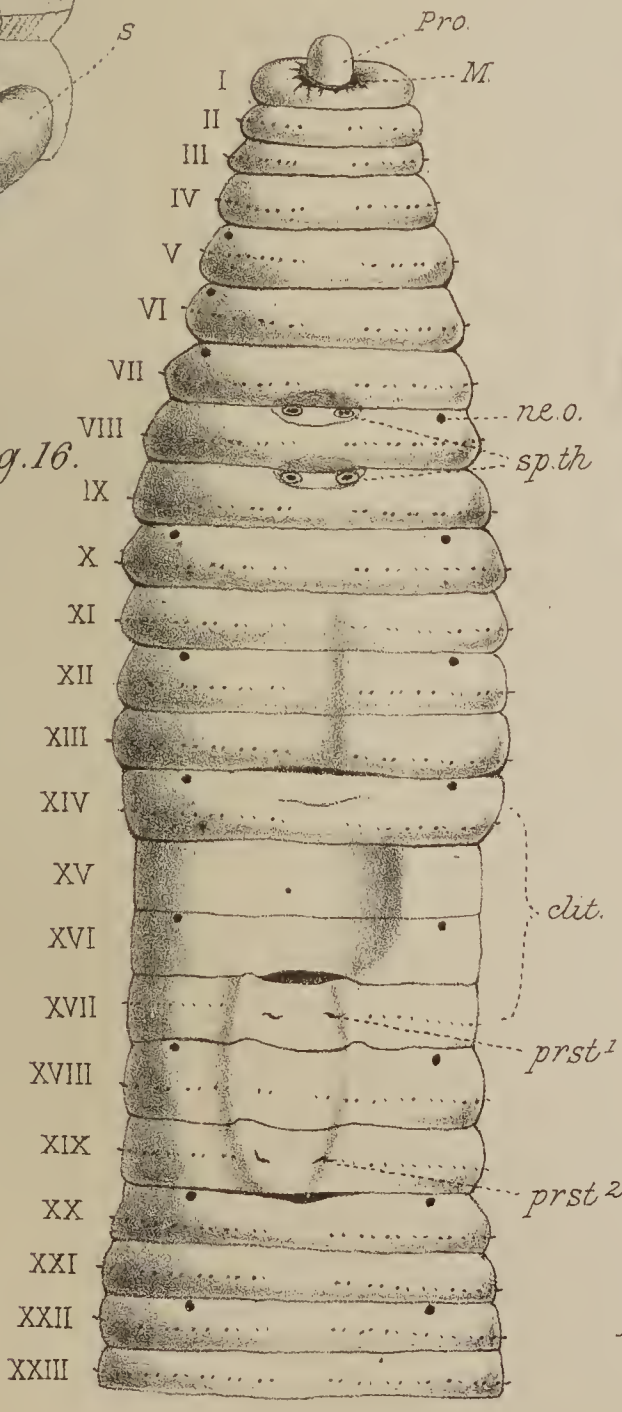

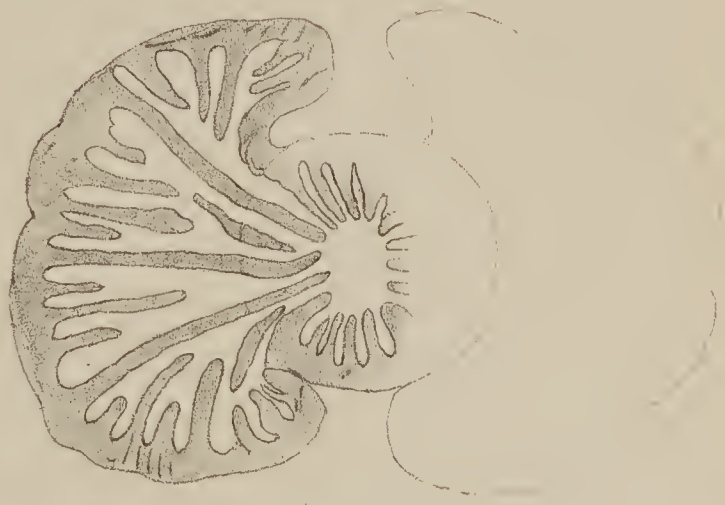

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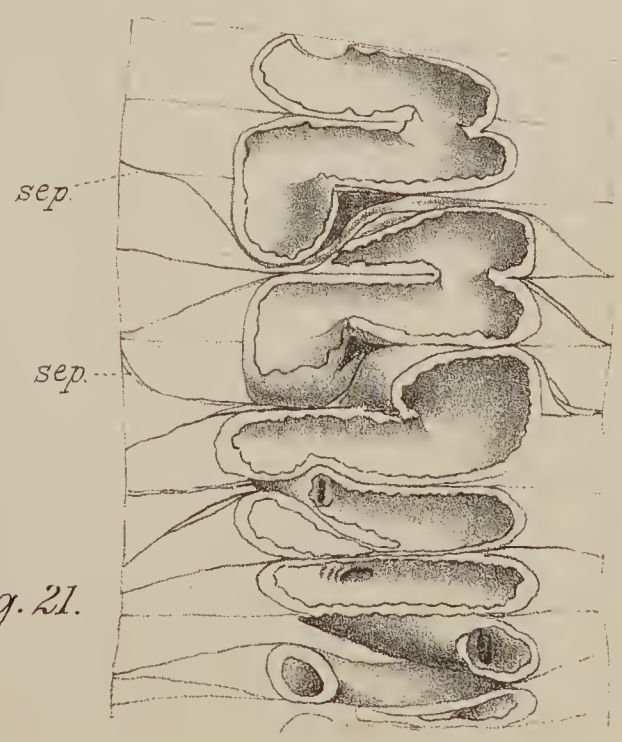


Fig. 21.

F. Huth, Lith^r Edin^r

Fig. 18.

Fig. 19.

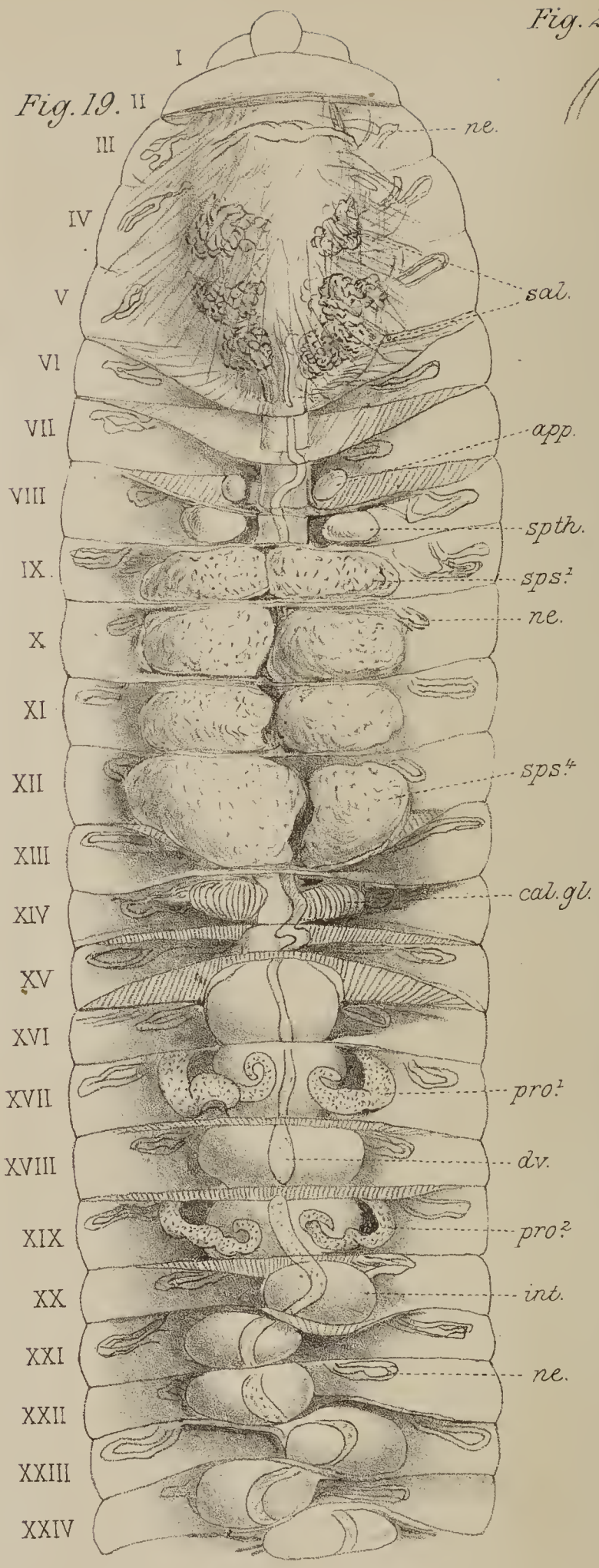


Fig. 24 a.

Fig. 25.

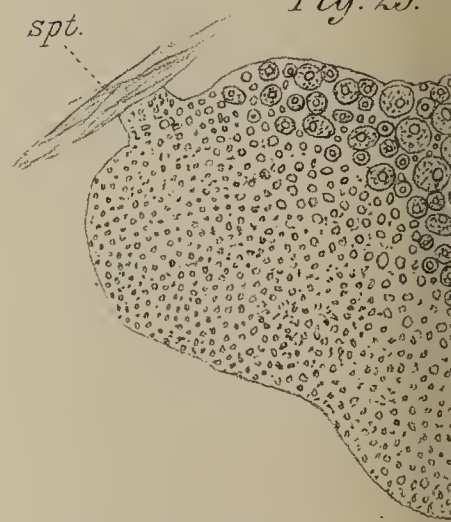
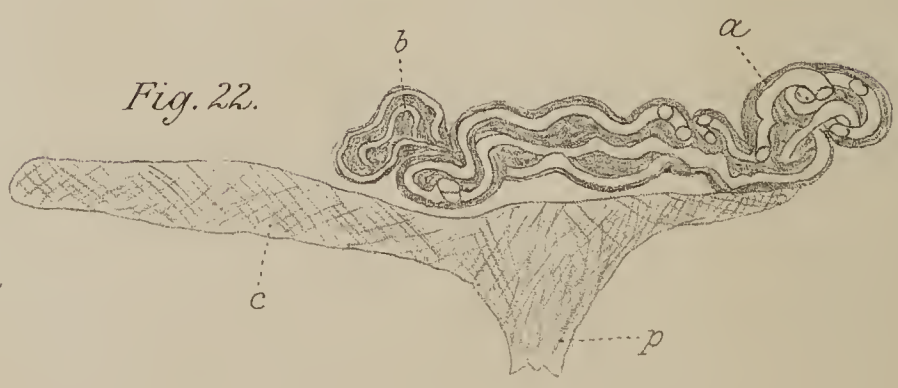


Fig. 28.

Fig. 23.

Fig. 22.



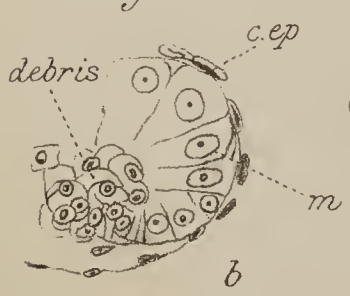


Fig. 29.

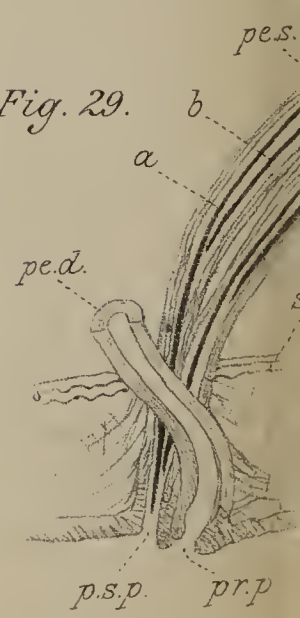


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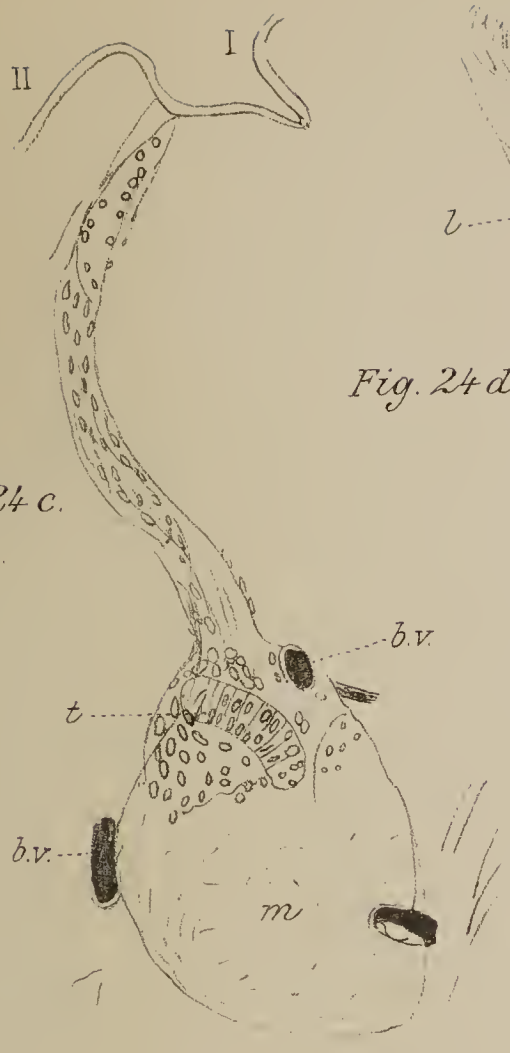
Fig. 24 c.



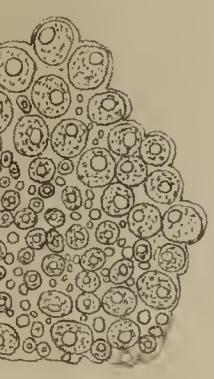
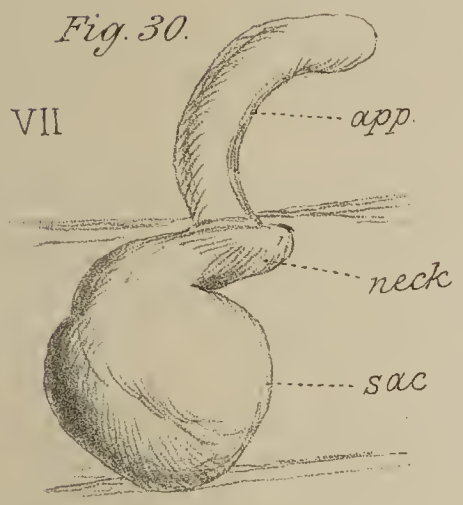


Fig. 30.



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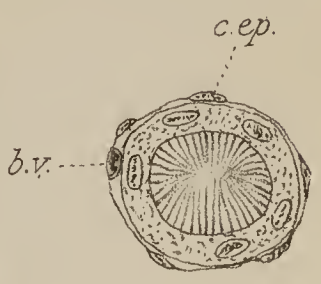


Fig. 27.

Fig. 26.

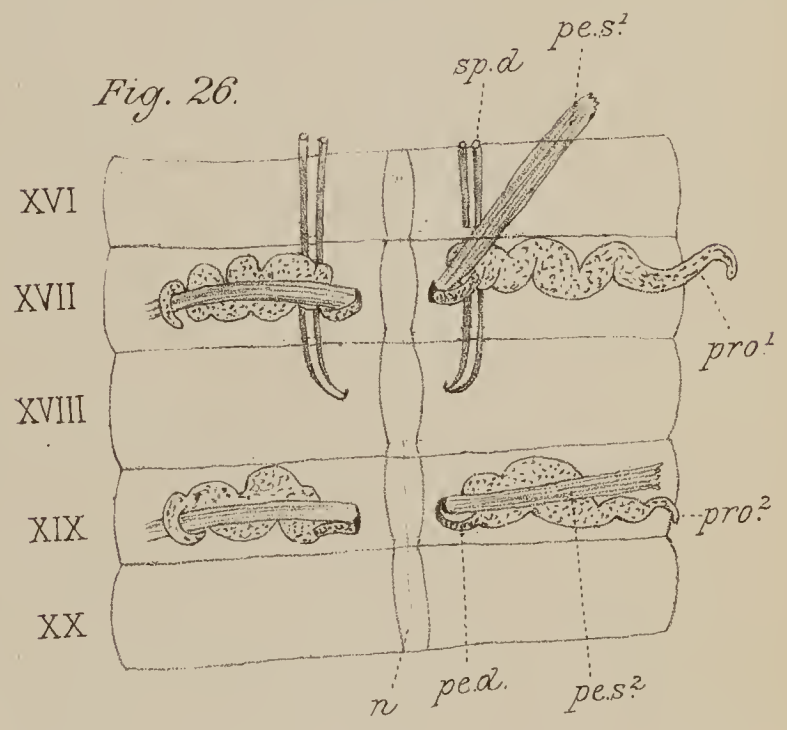


Fig. 31.

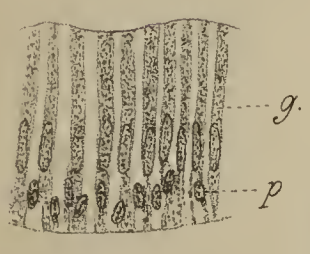
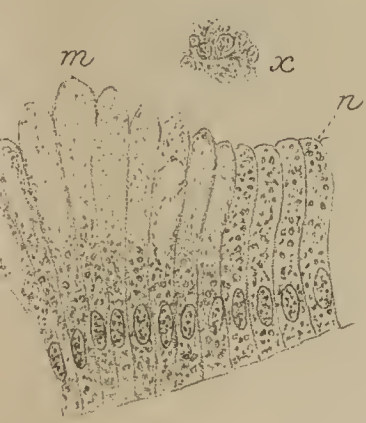
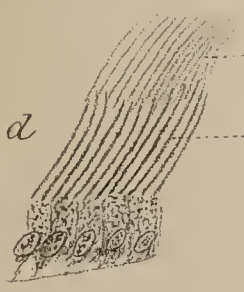


Fig. 32.





F. Huth, Lith^r Edin^r

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Note on a Large Squid (Ommastrephes pteropus, Stp.).

By

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On the 6th of January, 1892, Dr. Elliot of Kingsbridge most generously presented to the Marine Biological Association a large and interesting Cephalopod which was captured off Salcombe.

Dr. Elliot brought the squid to the Plymouth Laboratory, and it was subsequently purchased for the Oxford Museum by Prof. Ray Lankester, who requested me to identify it, giving me much kind help, for which I wish to express my sincere thanks.

The specimen in question, which I find to be a female *Ommastrephes pteropus*, Stp. (*Sthenoteuthis pteropus*, Verr.), is in very fair condition, having been preserved in chromic acid and in alcohol. The left eye is unfortunately missing, and the lateral membranes of the arms and lining of the siphon pit are somewhat torn. The principal measurements, which can only be approximate owing to the shrinking during preservation, are as follows :—Length from the extremity of the body to the edge of the mantle, dorsally, 51 cm.; length from the extremity of the body to the edge of the mantle, along the postero-ventral surface, 50 cm.; length from the extremity of the body to the level of the mouth, 66 cm. The edge of the mantle is nearly straight along its postero-ventral border, and is produced to a slight point dorsally at the end of the nuchal cartilage, as figured by Steenstrup (**3**, p. 146, fig. 3). The large "caudal fins" are transversely rhomboidal, as described and figured by Verrill (**5**, p. 229, and Pl. LIV, fig. 2 *a*). The breadth across the two is 40 cm.; they each measure 27 cm. along the posterior free edge, and 23 cm. along the dorsal line of attachment. The dorsal or first pair of sessile arms is 23 cm. long, and trapezoidal in section. The second pair is 28 cm. long, with a keel and a small lateral membrane, whose maximum width is about 1·5 cm., on the ventral border. The third or lateral pair of arms (Fig. 1) is 28·5 cm. in length; on the outer surface is a large keel, broadest

FIG. 1.

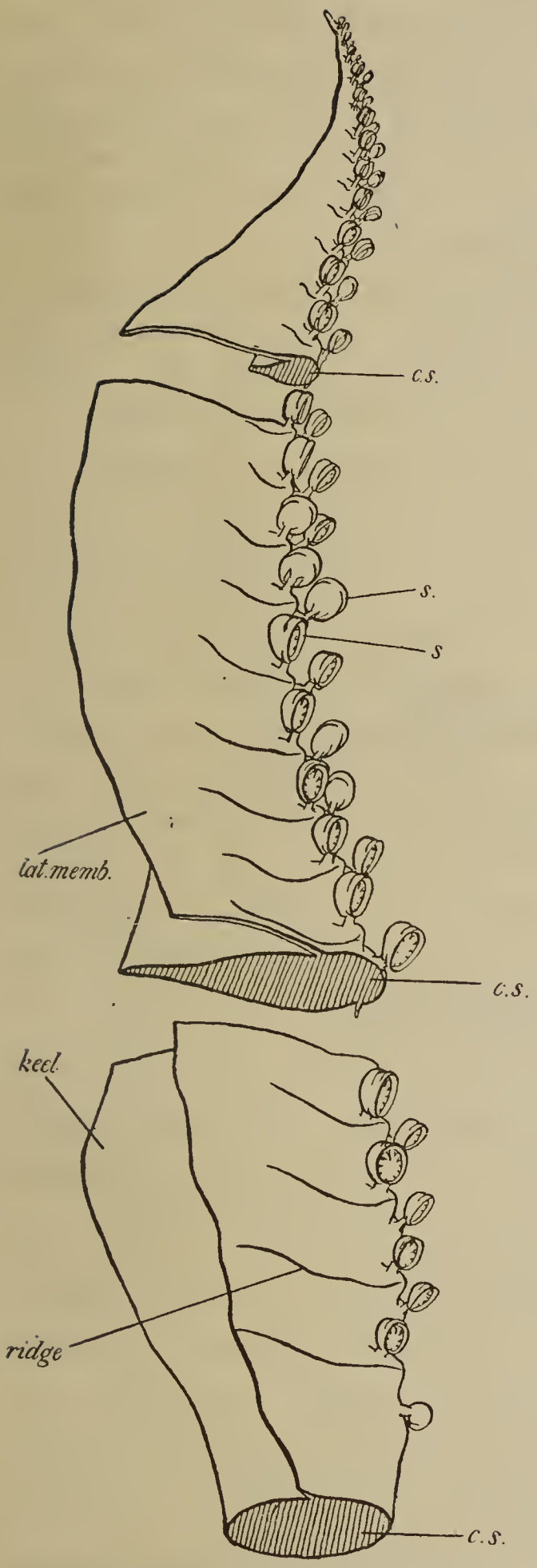

FIG. 2.

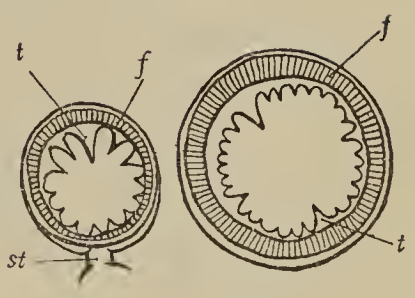

FIG. 3.

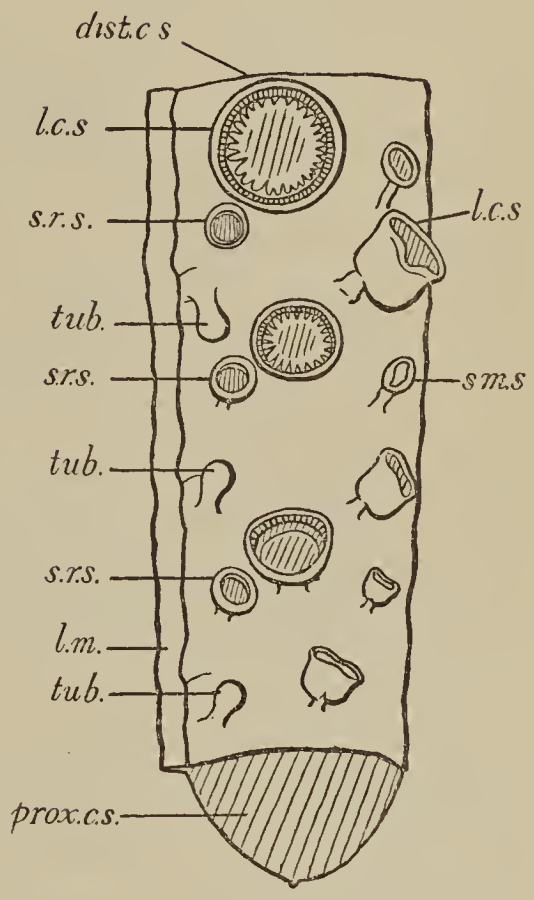

FIG. 1.—Posterior view of the third (left) arm. *Lat. memb.*, lateral membrane; *s.*, sucker; *c. s.*, cut surface. The arm is drawn diagrammatically, as if cut into three pieces.

FIG. 2.—On the left, figure of one of the suckers of the sessile arms. On the right, figure of one of the large suckers of the club of the left tentacle. *st.*, stalk or peduncle; *f.*, circular fold bearing horny plates; *t.*, teeth of horny margin.

FIG. 3.—View of the proximal part of the left tentacular club, diagrammatically drawn as if cut off. *Dist.c.s.*, distal cut surface; *prox.c.s.*, proximal cut surface; *l.c.s.*, large central sucker; *sm.s.*, small sucker; *s.r.s.*, smooth-rimmed sucker; *tub.*, tubercle; *l.m.*, lateral membrane.

below the middle of the arm. Along the postero-ventral edge of this arm extends a broad membrane (*Lat. memb.*, Fig. 1), about 5 cm. wide near the middle of the arm. This lateral membrane, which is formed by the extension of the platform on which are situated the suckers of the arm, is supported by thick ridges running out from between the suckers. The ventral or fourth pair of sessile arms is 28 cm. long, with a keel but no membrane.

All the sessile arms have along their inner surface two rows of suckers. One of these is figured (Fig. 2) to show the shape and disposition of the teeth of the horny margin (*t*, Fig. 2). A fold (*f*, Fig. 2) supporting horny plates runs round the inner edge.

The tentacular arms, 64 cm. long, are slender and clubbed. In Fig. 3 I have represented the proximal end of the club of the left tentacle as if cut off, in order to show the slight lateral membrane on the dorsal edge, and the small keel on the outer surface, which is more prominent towards the tip. There are two central rows of suckers (*l. c. s.*, Fig. 3), very large towards the middle of the club, and on each side a row of small long-stalked suckers (*s. m. s.*, Fig. 3), situated on the transverse ridges which run between the large suckers. In Fig. 2 is shown a large sucker in greater detail; round the rim internally is a circular shelf-like fold (*f.*, Fig. 2), bearing horny plates. The inner horny margin of the sucker is provided with teeth all round, four of which are large and prominent (*t.*, Fig. 2). At the proximal end of the club on the dorsal edge is the "connective apparatus," consisting of three smooth-rimmed suckers (*s. r. s.*, Fig. 3), alternating with three large tubercles (*tub.*, Fig. 3). The right tentacle bears a corresponding apparatus. The arrangement of these suckers and tubercles is similar to that described and figured by Steenstrup for *O. pteropus* (**2**, fig. 2, p. 81; and **3**, fig. 3).

From the last suckers on the club to within 15 cm. of the base of the tentacle are fourteen transverse ridges on the inner surface; they disappear gradually towards the base. Below the buccal membrane, which is provided with seven points, is a cavity communicating with the exterior by two apertures at the base of the dorsal arms, and two apertures at the base of the tentacles. Outside the base of the tentacles are two pits, or pockets.

The funnel is represented in Fig. 4 as bent back, so as to expose the pit in which it lies. It is retained by four bridles, two towards the middle line (*in. br.*, Fig. 4), and a thicker bridle on each side (*out. br.*, Fig. 4). Within the bases of attachment of the inner bridles are seen two apertures (*d. ap.*, Fig. 4), communicating with the cavity of the siphon above the valve.* Inside the external bridle is an aperture, perhaps artificial, communicating from the siphon pit

* I have observed these apertures in *Thysanoteuthis rhombus*.

to the cavity outside the bridle, which opens by the "ouverture anale" of D'Orbigny (1, p. 342). At the top of the siphon pit are seen folds which correspond pretty closely, but not exactly, to those figured for this species by Steenstrup (2, p. 79, fig. 1). There are

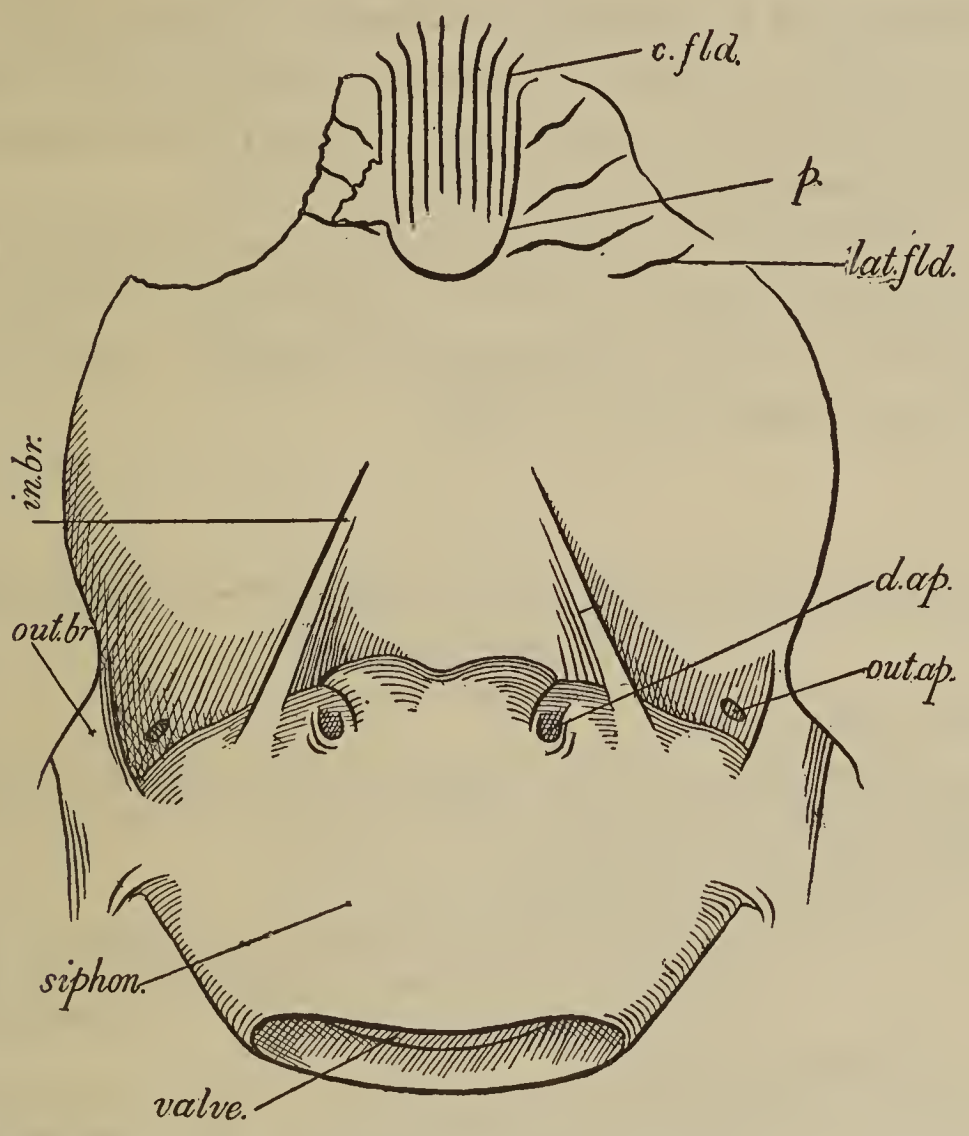

FIG. 4.—View of siphon pit, the siphon being bent down so as to expose it. *out. br.*, outer bridle; *in. br.*, inner bridle; *out. ap.*, outer aperture; *d. ap.*, aperture in dorsal or inner wall of siphon; *c. fld.*, central fold; *lat. fld.*, lateral fold; *p.*, shallow pocket or velum.

eight grooves within the central space, bounded by a U-shaped fold or velum, and four folds on either side outside it. Steenstrup figures only twelve folds in all.

The specimen before us, then, agrees with Prof. Steenstrup's species, *O. pteropus*, in size, in having very well-developed lateral membranes to the arms, a nearly straight mantle edge, numerous folds in the siphon pit, and in possessing a particular arrangement of the connective apparatus. This species, which inhabits the Atlantic, has rarely been recorded from our shores. Mr. E. A. Smith, of the British Museum, has kindly given me the following information concerning two specimens now in the Natural History Museum. One is an incomplete specimen obtained on November 19th, 1883, at Scarborough: it was 52 inches long (arms included), 25 inches in girth, and 22 inches across the fins. The second specimen is a perfect one, captured in the North Sea, February 27th,

1884. It measures from the mouth to the end of the body 39 inches; in girth 22 inches; across the fins 23 inches. The tentacles are 36 inches in length.

I have added to this note a table of the chief diagnostic characters of the well-established genera of living Oigopsid Cephalopods. It is not an attempt at a natural classification of these genera, but only a tabular statement of their characters, which may, I hope, be of some use in identifying specimens—a task by no means easy now, owing to the literature being much scattered.

For the full literature of the subject, synonyms, &c., I must refer the reader to Mr. Hoyle's excellent Catalogue of Recent Cephalopoda, published in the "Challenger" Reports, and in the Proc. Roy. Phys. Soc. Edin. vol. ix, 1886.

Table of the Chief Characters of the Genera of Recent Oigopsid Cephalopods.

A. Siphon without valve.

A. Siphon without bridles. Mantle attached to head by 3 bands. Three dorsal pairs of arms, more or less webbed.

a. Fins rounded. Eyes sessile.

a[1]. Pen simple, lanceolate.

1. Arms with 2 rows of smooth-rimmed suckers. Tentacles with smooth-rimmed suckers and slight membrane. Mantle covered with chitinous papillæ. Cranchia (Leach, 1817).

b[1]. Pen with cone.

2. Arms with 2 rows of suckers. Club of tentacles with 4 rows of blunt-toothed suckers, and group of suckers and tubercles forming connective apparatus. Prominent eyes. Seven lobes to buccal membrane. Taonius (Stp., 1861).

3. Arms short, with 2 rows of suckers. Tentacles absent in adult. Eyes prominent. Two rows of cartilaginous papillæ on mantle. Leachia (Les., 1821).

b. Pen lanceolate. Fins more or less angular. Eyes pedunculate.

4. Arms with 2 rows of stalked suckers. Tentacles with 2 rows of suckers along the stem and 4 on the club. Suckers all smooth. Eyes pedunculate (sessile in type species?). Fins terminal. Loligopsis (Lam., 1812). [Zygœnopsis, de Roche., 1884.]

5. Arms with 2 rows of sessile suckers. Tentacles long, with tubercles along stem. Fins triangular and subterminal. Pyrgopsis (de Roche., 1884).

B. Siphon with 2 bridles.

6. Arms with 2 rows of toothed suckers. Club of tentacle with 4 rows of toothed suckers. Siphon pit with velum. Pen with cone. Seven lobes to buccal membrane. Eye with sinus. Fins rounded. Steenstrupiola (Pfeffer, 1884).

B. Siphon with a valve.

A. Siphon without bridles.

7. Arms with 4 rows of smooth suckers. Club of tentacle with many rows of minute suckers. Small sinus. Pen feather-shaped. Suckers on the 7 lobes of buccal membrane. Fins subterminal, rounded. Bathyteuthis (Hoyle, 1885).

B. Siphon with 1 bridle (probably 2 fused).

8. Three dorsal pairs of arms, webbed. Socket I-shaped. Pen feather-shaped. Fins rounded. Histiopsis (Hoyle, 1885).

C. Siphon with 2 bridles.

a. Ear-shaped socket of mantle.

a^1. No sinus. Fins subterminal and rounded. Ventral arms large and with lateral membrane.

9. Arms very unequal, 2 rows of toothed suckers to first 3, and 1 row to ventral arms (?). Club of tentacle with sessile suckers and membrane, 4 rows down the stem. Spoon-shaped olfactory organ. Pen with hollow cone. Doratopsis (de Roche., 1884).

10. Arms with 2 rows of toothed suckers. Tentacles extremely long, suckers along stem, large club with long curved toothed suckers and spoon-shaped extremity. Buccal membrane with 7 lobes. Six buccal aquiferous openings. Spoon-shaped olfactory organ. Pen lanceolate. Cheiroteuthis (d'Orb., 1839).

b^1. Small sinus. Lateral membrane of arms very small.

11. Arms with 2 rows of nearly smooth suckers. Tentacles long and lash-like, numerous minute toothed suckers at end. Six lobes to buccal membrane. Pen narrow, with cone. Fins rhomboidal. Socket without pronounced tooth.
Mastigoteuthis (Verrill, 1881).

b. I-shaped socket (except Ancistrocheirus ?)

a^1. Without sinus.

a^2. Fins of separate filaments.

12. First 3 pairs of arms with 4 rows of smooth suckers. Ventral arms with 2 rows, and lateral membrane. Club of tentacles with many rows of smooth suckers. Fins of muscular filaments joined only at base. (Small sinus ?).
Chtenopteryx (Appelöf, 1888).

b^2. Fins rhomboidal. Pen lanceolate.

13. Arms with 2 rows of toothed suckers. Tentacles long and slender, with suckers along whole length; club with lateral membrane and numerous small suckers. Lobes of buccal membrane indistinct.
Brachioteuthis (Verrill, 1881).

c^2. Fins rounded.

a^3. Pen with cone.

14. Arms with 2 rows of suckers, smooth proximally and toothed distally. Club of tentacle with 4 rows of smooth suckers and group with tubercles (conn. app.). Buccal membrane with 7 lobes. Pen broad, hollow, bent at tip, and with small cone. Calliteuthis (Verrill, 1880).

b^3. Pen lanceolate.

15. Arms with 2 rows of suckers, the 3 dorsal pairs of arms joined by a web, and the ventral joined by a web. Tentacle with 6 rows of toothed suckers on club, and conn. app. extending down the stem, cluster of smooth suckers at tip. Four buccal and 2 brachial aquiferous openings. Buccal membrane with 6 lobes.
Histioteuthis (d'Orb., 1839).

b^1. With sinus.

a^2. Without hooks.

a^3. Pen with cone. Nuchal crests small or absent.

16. Arms with 2 rows of toothed suckers and slight web. Club of tentacle with 4 rows of toothed suckers distally and 10 rows of smooth suckers proximally. Buccal membrane with 7 lobes. Fins rounded.
Tracheloteuthis (Stp., 1881).

17. Arms with 2 rows of toothed suckers. Club of tentacles with 4 rows of toothed suckers and lateral membrane. Conn. app. extending along the stem, cluster of smooth suckers at tip. Fins forming an arrow-head.
Architeuthis (Stp., 1856).

b^3. Pen lanceolate. Nuchal crests.

18. Arms with 2 rows of smooth suckers. Tentacles mere stumps. Chaunoteuthis (Appelöf, 1890).

b^2. With hooks. Fins rhomboidal. Conn. app. at base of club, and generally group of suckers at tip.

a^3. Pen lanceolate.

a^4. Fins terminal. Suckers to tentacles.

19. Arms with 2 rows of hooks. Tentacles short, suckers few. Pen slender, cartilaginous. Fins somewhat rounded, terminal. Verania (Krohn, 1847).

b^4. Fins subterminal generally. Hooks to tentacles.

a^5. Hooks to arms and tentacles. Very large fins.

20. Arms with 2 rows of hooks. Tentacles with hooks on club. Fins large, along nearly whole length of mantle, subterminal. Socket ear-shaped (?). Ancistrocheirus (Gray, 1849).

b^5. Hooks and suckers to arms and tentacles.

21. Arms with 2 rows of hooks and a few suckers. Club of tentacles with hooks. Buccal membrane with 8 lobes. Fins slightly rounded. Enoploteuthis (d'Orb., 1839).

22. Arms with 1 row of hooks near base and 2 rows of suckers near tip. Club of tentacles with alternate hooks and suckers. Abralia (Gray, 1849).

b^3 Pen with cone.

a^4. Only suckers on arms in 2 rows. Hooks and suckers on tentacles. Buccal membrane with 7 lobes.

23. Arms with two rows of smooth suckers, and lateral membrane. Club of tentacle with 2 rows of hooks. Two brachial and 6 buccal aquiferous sacs. Solid cone to pen. Onychoteuthis (Licht., 1818).

24. Arms with two rows of suckers. Club of tentacles with 2 inner rows of hooks, and 2 outer of toothed suckers. Cone of pen solid at apex. Teleoteuthis (Verrill, 1882).

25. Arms with 2 rows of smooth suckers. Club of tentacles with 2 rows of hooks. Cone of pen hollow. Ancistroteuthis (Gray, 1849).

b^4. Hooks and suckers on arms in 4 rows.

26. Ventral arms with 4 rows of suckers, the other arms with 2 rows of hooks within and 2 rows of suckers without. Hooks on tentacles. Buccal membrane rounded. Pen with hollow cone. Fins reach beyond tip of body. Gonatus (Gray, 1849).

c. Socket with large tooth or process.

27. Arms with 2 rows of toothed suckers and lateral membrane. Club with 4 rows of toothed suckers and conn. app. extending along the stem. Sinus. Two apertures at back of siphon. Pen lanceolate. Long fins along whole length of the mantle. Thysanoteuthis* (Troschel, 1857).

D. Siphon with 4 bridles, and 2 apertures at back. ⊥-shaped socket. 2 brachial, 2 anal, and 4 buccal aquiferous openings. Buccal membrane with 7 lobes. Three longitudinal nuchal crests. Eye with sinus. Pen with hollow cone. Arms with 2 rows of toothed suckers.

a. Folds in siphon pit absent, or only within the velum.

28. Smooth siphon pit. Little or no lateral membrane to arms. Teeth absent or blunt on large suckers of club. Illex (Stp., 1880).

29. Folds in siphon pit within the velum. Lateral membrane of arms small. Alternate sharp and blunt teeth on one half the circumference of large suckers of club. Todarodes (Stp., 1880).

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* A small specimen of Thysanoteuthis rhombus, Trosch., presented to the Oxford Museum by Prof. Ray Lankester, appears to possess 4 bridles; this may perhaps be due to the artificial splitting of a single pair.

b. Folds in siphon pit within and without the velum. Lateral membrane of arms large. Large suckers of club with 4 large teeth, and small teeth all round.

30. Suckers of arms moderate in size and number.
Ommastrephes (d'Orb., 1835).

31. Suckers of arms long-stalked and crowded.
Dosidicus (Stp., 1857).

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4. Verrill, *Ceph. N. E. America,* Trans. Connect. Acad., vol. i, part 1, 1880.

The Oscula and Anatomy of Leucosolenia clathrus, O. S.

By

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With Plate XXIX.

As is well known, Leucosolenia clathrus is a sponge in which the oscula have been hitherto supposed to be conspicuous by their absence. In Haeckel's "Kalkschwämme" will be found a full description of this sponge, together with an account of all observations upon it published previously to the publication of that monograph. The following is a summary of Haeckel's description; for further details I refer to the monograph itself.

Leucosolenia (Ascetta) clathrus was first described by Oscar Schmidt,[1] in 1863, as follows:—"Grantia ramosa, ramis 1 mmtro. latis, paulum compressis, varie et irregulariter implexis. Oscula in summitate ramusculorum brevium. Spicula triradiata, radiis obtusis. Color læte sulphureus." Later[2] Oscar Schmidt corrected his former description, and stated that though he formerly thought he had found oscula with a simple lens, he was unable to find them now with a "compositum." He further stated that he was unable to find a trace of a canal system in this sponge; the trabeculæ (Balken) composing it consisted of two very different layers, an outer colourless one containing the spicules, and an inner

[1] 'Spongien des adriatischen Meeres,' Suppl. I, p. 24

[2] Op. cit., Suppl. II, p. 8.

yellowish granular mass without spicules, filling up the whole space which in Leucosolenia botryoides constitutes the ramified cavity. Then Gray made this sponge the type of a new genus, Clathrina, which he characterised by simply translating the original Latin diagnosis of Schmidt given above.

Haeckel finds that Oscar Schmidt was in error in describing the sponge as solid, and as the result of his studies he divides his Ascetta clathrus into four varieties. (1) Ascetta labyrinthus, with a single layer of endoderm-cells, and no endogastric septa or partitions. (2) A. mæandrina, with the endoderm thickened to form a stratified epithelium of several cell layers, the uppermost bearing flagella. No endogastric septa or partitions. (3) A. clathrina, with the endoderm forming a stratified epithelium as in mæandrina, and the gastric cavity divided by partitions in which the embryos develop. (4) A. mirabilis, the colony consisting partly of A. labyrinthus and partly of A. clathrina. In A. labyrinthus alone did the spicules lie in a single layer; in the other three varieties they formed several layers. The plexus of the anastomosing tubes was much looser and with wider meshes in A. clathrina than in A. labyrinthus and mæandrina, and the tubes themselves averaged a larger diameter (1—2 mm., sometimes 3—5 mm.) in the two latter varieties than in the former (where they measured 0·5 to 1 mm., seldom more). In A. labyrinthus and mæandrina the tubes were much twisted and contorted, reminding one of the gyri of the mammalian brain. In all forms alike Haeckel found the colonies completely devoid of oscula, Auloplegma forms. He also at first thought he had seen oscula, but found he had mistaken artificial openings for such. Even the Olynthus forms were without openings, Clistolynthi. Since Haeckel's monograph I know of no work dealing with the question of the lipostomy and variations of this interesting and beautiful sponge. Metschnikoff[1] describes the histology

[1] "Spongiologische Studien II: Anatomisches über Ascetta," 'Zeitschr. f. wiss. Zool.,' xxxii, 1878-9, pp. 358—362.

with great accuracy, but says nothing of the oscula, though since he talks of "Tarrus forms" it might be inferred that he had seen them. Oscar Schmidt's work[1] on the development of this form contains no mention of oscula.

The curious phenomenon which is usually termed lipostomy has always been a great puzzle to me. How can a sponge exist without an osculum? The osculum is the central exhalent opening of the whole canal system, and to it converge all the currents which enter by the pores and flow along the canals. How can so important an opening be wanting? Haeckel attempts an answer to the question in the case of this sponge: "In the interior of the tubes the water goes in and out only by the pores."

Wishing to study the histology of this sponge, I was able, by the kindness of Sig. Lo Bianco, the well-known Conservator of the Naples Zoological Station, to go with the little steamer "Frank Balfour," of the Station, in order to collect and preserve Leucosolenia material fresh from the sea; and in the very first specimen of Leucosolenia clathrus which came on board I saw oscula of such a size that I was perfectly astounded. To be brief, I find that Leucosolenia clathrus in the fresh healthy condition not only has oscula, but in the full-sized specimens larger oscula than any other Leucosolenia known to me, whether from pictures or in the flesh.

The specimens of Leucosolenia clathrus may be for convenience divided into "large" and "small." By large specimens I mean the big, full-grown colonies, often 10 cm. in length and 3 or 4 cm. in height. By small specimens I mean the very young colonies of 5 mm. or less in extent. Fig. 1 represents two oscula of a large specimen seen in profile, natural size; one osculum (*a*) is widely open, the other (*b*) is partly contracted. Fig. 2 represents three more oscula from the same specimen (which had altogether ten oscula), seen

[1] "Das Larvenstadium von Ascetta primordialis und Ascetta clathrus," 'Arch. f. mikr. Anat.,' vol. xiv, 1877, pp. 249—263, Taf. xv, xvi.

from above. Fig. 4 represents the whole of a small colony with three oscula, magnified five times linear. It will be seen that the small colony forms a more or less flat plexus of narrow tubes, from which chimney-like oscular tubes arise of about 0·325 mm. in diameter. In fact, it grows in precisely the same manner as the specimens of Leucosolenia coriacea at Plymouth, in which I observed and described a sieve membrane over the oscular opening.

If now we study the edge of one of the larger oscula with a lens by transmitted light, we see that it has a margin of about half a millimeter in width where the wall is more transparent than in other parts of the oscular tube, and a very short distance above where this more transparent part begins an opaque line can be seen running round the whole osculum (fig. 2 *a*, *s*.).

This clearer margin indicates the line at which the collared endoderm stops short, so that the clearer margin is lined with ectoderm within and without, while the more opaque part of the oscula tube is lined by collar-cells on the inner side. The opaque line *s* is a muscular sphincter, by the contraction of which the osculum can be closed, and occurring alike in the larger and in the smaller oscula.

To proceed now to the study of sections and preparations. Fig. 6 *a*, *b*, *c*, *d*, represent four sections from a continuous series through one of the oscula of the sponge represented in fig. 4, after hardening in $\frac{1}{2}$ per cent. osmic acid, soaking for an hour (on the slide) in picro-carmine, in order to counteract the blackening of the osmic acid, and finally staining with hæmatoxylin. *a*, *b*, and *c* are three sections about the middle of the series, *b* being the next section after *a*, and *c* the next but one after *b* ; while *d*, in which the osculum is cut tangentially, is the thirteenth section after *a*. In all the sections the spicules have been carried by the edge of the razor towards the left, injuring the ectoderm a little.

Fig. 6 *a* shows well the general structure of the oscular wall. The collar-cells stop short suddenly at a point, and it can be seen plainly in figs. 6 *a* and *c* that they are continued

directly by the flattened ectoderm-cells. In some sections (6 *b*) it looks as if there was an intermediate form of cell; but I am convinced that this is only due to ordinary collared cells being cut obliquely, so that only their bases are seen. A short distance above where the collar-cells stop, the sphincter is seen projecting like a ledge into the interior. Above it the ectoderm goes on for a considerable distance. The height of this oscular margin, formed only of two layers of ectoderm with some spicules and amœboid cells between, is really remarkable.

Fig. 7 *a* represents the sphincter of one of the larger oscula in section (the two sides of the oscula are of course not drawn at their natural distance apart, for then they would have to be separated by more than the length of the whole plate). 7 *b* is another section, rather thick, from the same series, showing the sphincter, which was a little crumpled, cut tangentially and obliquely. This osculum had been hardened with a saturated solution of corrosive sublimate in absolute alcohol, and the sections stained on the slide with borax carmine first, and then with hæmatoxylin, a method which I find exceedingly good for showing the ectoderm. Fig. 8 represents a transverse section of the sphincter of another osculum, prepared by the osmic-picro carmine-hæmatoxylin method.

The sphincter, as can be seen, projects as a ring-like ridge into the interior of the osculum. We shall consider its minute structure presently. When this sphincter contracts it closes the osculum, which then, in the large colonies, has a very characteristic shape, which I do not know how to describe better than by comparing it to the human breast (fig. 3). In such a breast-shaped osculum the nipple is formed by the ectodermal margin of the osculum, and at the base of the nipple one finds the contracted sphincter. Fig. 9, *a*, *b*, and *c*, represent sections from a series through the osculum represented in fig. 3, hardened in abs. subl.,[1] and stained with borax carmine and hæmatoxylin.

[1] I use this as a convenient abbreviation for a saturated solution of corrosive sublimate in absolute alcohol.

To return now to this sphincter. It consists of two layers of fusiform ectoderm-cells arranged tangentially, between which one finds at intervals some of the large amœboid mesoderm-cells which occur throughout the sponge, but they are by no means common in the sphincter. The point I wish to emphasize is that the contractile muscular cells are the epithelial ectoderm-cells.

The simple two-layered nature of the sphincter is apparent from the transverse sections 6 *a*, *b*, *c*, 7 *a*, 8; but still more so from the tangential sections 6 *d*, 9 *a*, and *c*; less so in the thick section 7 *b*. Perhaps an even more convincing method of seeing it is to put a piece of the wall of a fresh living osculum into Ranvier's one third alcohol for twenty-four hours, and then to carefully pull the sphincter off with a needle and examine it laid out flat in glycerine, after previous staining with picro-carmine. In such a preparation one sees, by carefully focussing its surface, a layer of nuclei. If now the microscope be focussed deeper the layer of nuclei first seen vanishes, and a distinct layer of similar nuclei takes their place. There is absolutely no other cell layer but these two, unless one happens to find one of the scattered amœboid cells, which are by no means common.

These flat preparations offer the best means of studying the nature of the cells, and I find them differ on the opposite surfaces of the sphincter. On one surface they are spindle-shaped, elongated, and with distinct cell outlines. The spherical nucleus is surrounded by granules which form a fusiform figure, extending towards the two ends of the cell. Cells of this kind are shown in fig. 12. On the other surface the cells have similar nuclei, but no distinct cell outlines; the granules are sometimes arranged in a fusiform figure, sometimes not, but are much fewer relatively. Cells of this kind are shown in fig. 11. By focussing the preparation deeper from which fig. 12 was drawn, I could see cells similar to those represented in fig. 11; and similarly by focussing the preparation drawn in fig. 11, I could see cells like those in fig. 12. I have tried to represent this point more clearly in fig.

13, *a* and *b*. In the middle of each drawing is seen one of the amœboid wandering cells, one and the same cell both in 13 *a* and 13 *b*. Now 13 *a* is drawn with the microscope at the lower focus, and shows the fusiform cells; while 13 *b* is drawn at the upper focus, and shows the other kind of cells. 12 *a* represents one of the second kind of cells macerated out from the same preparation from which fig. 12 was drawn. I take it that the fusiform cells are more specially differentiated ecto-derm-cells, while the other kind are more ordinary ectoderm-cells. In transverse sections of the sphincter the cells on one surface commonly appear more rounded and project higher than on the other (figs. 7 *a*, 8). I believe that the rounded projecting cells are the fusiform cells of the flat preparations, and the flat cells the others. It is difficult to be certain of this point; I infer it from the fact that in such sections the ronnded cells are closer together than the flat ones. The two kinds of cell appear to occur indifferently on one or the other side of the sphincter. From the left side of fig. 7 *a*, it would appear as if both sides of the sphincter might, in places, be formed only of fusiform cells.

The nuclei of the cells composing the sphincter have a similar structure in both kinds of cells. They are spherical or slightly ovate, measuring in glycerine preparations about 6·5 μ, in Canada balsam preparations (prepared in all points in the same manner as the glycerine ones) about 5·2 μ. The nucleus rarely has one distinct nucleolus; more usually several small ones. In preparations hardened with Hermann's fluid, and stained by Flemming's method[1] with saffranin, gentian violet, and orange G., the structure of the nucleus is well shown, especially if the sections are cut very thin (4 or 5 μ). Then the whole nucleus is seen to be filled with a fine network, which may be thickened at several nodal points, sometimes greatly at one, producing the appearance of a nucleolus. Without entering at present into further histo-

[1] Vide his paper in the 'Arch. f. mikr. Anat.,' vol. xxxvii (1891), "Ueber Theilung und Kernformen bei Leukocyten, und über deren Attractionssphären," p. 296.

logical details, I will state merely that these nuclei exactly resemble in size, structure, and appearance the nuclei of the remaining ectoderm, and differ in precisely these three points from the nuclei of the endoderm, still more so from the nuclei of the amœboid mesoderm-cells. The granules of the cells appear when carefully focussed as round black spots, but when the microscope is a little high or too low they appear as minute black rings round a central clear spot, and in sections often look not unlike fibrillæ cut transversely, which of course is not the case.

Thus, to recapitulate, this sphincter is composed of two layers of ectoderm, with a few scattered amœboid cells between, and the contractile cells are the ectodermal epithelium. Thus, in one of the simplest existing types of sponges, I have arrived at the same result as Topsent,[1] who in his work on the Clionidæ, finds that the ectodermal or endodermal "cellules de revêtement" are the contractile elements. The sphincter of the oscula of Leucosolenia clathrus is an especially favorable object in which to study this question, as the cells are so large compared with the minute cells of siliceous sponges, and the sphincter itself can be so easily prepared out or cut into sections. We have in this sphincter perhaps the most primitive type of muscle-cell in the animal kingdom; it can hardly be called a myo-epithelial cell, it is still a simple ordinary epithelial cell.

Various authors[2] have described muscle-cells lying in the mesoderm; and until Topsent wrote, I think I am right in saying that muscular cells in sponges were regarded as mesodermal. There is no reason why, in a highly differentiated sponge, muscle-cells originally forming part of an epithelium should not become more specialised and sink into the meso-

[1] "Contributions à l'étude des Clionides," 'Arch. de Zool. expér. et gén.,' tome v bis, Suppl. (1877—1890), p. 24, et seq.

[2] Vide Sollas's article "Sponges," 'British Encyclopædia;' "Monograph of the Tetractinellida," '"Challenger" Reports,' p. 42; von Lendenfeld, "Beitrag zur Kenntniss des Nerven- und Muskel-systems der Hornschwämme," 'S. B. k. pr. Akad. Wiss.,' Berlin, Nov. 12th, 1885.

derm. But the muscle-cells described by Topsent and in this paper make it, I think, to say the least, extremely probable that all muscular cells in sponges are of epithelial origin.

Dr. von Lendenfeld has published,[1] at divers times and in divers places, a classification of the Cœlenterata into Mesodermalia (sponges), in which the principal organs are derived from the mesoderm; and Epithelaria (other Cœlenterates), in which the principal organs are derived from the epithelia.

What are the principal organs of a sponge? I presume the ciliated chambers, skeleton, genital products, and the various kinds of muscle-cells, gland-cells, nerve-cells, &c. The skeleton certainly appears to be mesodermal, as far as we can judge, and perhaps also the genital cells. On the other hand, the ciliated chambers are almost certainly endodermal, and the muscle-cells of epithelial origin. There does not appear to be the slightest reason why the nerve-cells, so often described by von Lendenfeld, should (if they exist) be of mesodermal and not of ectodermal origin, as in other groups of animals; and the same may be said of their gland-cells. Thus it appears that the only principal organs of a sponge which can with any certainty be said to be of mesodermal origin are the connective-tissue system and the generative elements.

To return, however, to our oscula. We have in this sphincter a mechanism for closing the osculum, and in the sieve membrane over the oscula of Leucosolenia coriacea we have, I do not doubt, a structure which can be employed for a similar purpose, since Auloplegma forms of the latter sponge are so common. I look upon this as a good instance of two structures physiologically similar, but morphologically quite different. In my paper on the sieve membrane[2] I explained it as probably arising as a breaking through of the gastral cavity to the exterior in several places during the formation of the osculum, and hence as consisting of ecto-

[1] 'Monograph of the Horny Sponges' (London, 1889), p. 889; 'Proc. Zool. Soc.,' London, 1866, p. 566; 'Biol. Centralbl.,' ix, 1889, pp. 113—127, &c.

[2] "Note on a Sieve-like Membrane across the Oscula of a Species of Leucosolenia, &c.," 'Quart. Journ. Micr. Sci.' (n. s.), Part 2, January, 1892.

derm externally and endoderm internally. I see as yet no reason why I should depart from that opinion. On the other hand, it can hardly be doubted that the sphincter here described arises as a simple ingrowth of ectoderm, and consists of this layer only on both faces. In the young forms the sphincter shows only one or two cells on either face in transverse section (fig. 7, *a*, *b*, *c*), while in the older ones it consists of a great number lying side by side (figs. 7 *a*, 8, 11, 12, 13), so that it evidently grows with the osculum. I have not yet found an osculum devoid of a sphincter, but it is very probable that the young Olynthus would have none.[1]

In specimens of this sponge fresh from the sea the oscula were, as I have said, exceedingly conspicuous.[2] How is it these oscula have not been found before? I selected on my first collecting trip several large specimens of the sponge with widely open oscula, and put them into a separate vessel in sea water. What was my astonishment, however, when I got back to the Zoological Station, to find no trace of oscula in any of my specimens, not even an elevation to mark where they had been! The thin delicate walls of the sponge had completely collapsed, and the whole presented a shrivelled appearance, as different from the beautiful outlines and transparent yellow colour of the fresh living sponge as anything could be imagined. On a second occasion I selected another very fine specimen, and put it in a separate vessel, and brought it back with great care, changing the water several times on the way home. It was, however, of no avail; it arrived in the same shrivelled condition. The only indication that these sponges

[1] Since Haeckel observed only Clistolynthus forms it is possible that even the Olynthus has a sphincter. On the other hand, it would be quite possible for an Olynthus to contract itself completely without any special sphincter. Vide Metschnikoff's figure of a Clistolynthus of Ascetta blanca in longitudinal section, 'Zeitschr. f. wiss. Zool.,' xxxii, 1878–9, Taf. xxii, fig. 9.

[2] I cannot but express my astonishment that Haeckel did not see them, since he tells us in his monograph (p. 33) that he found this sponge growing in great quantities in a little bay (San Clemente) on the south side of the Spalmadori Cliffs on the coast of Lesina in 1871, and collected in a short time several hundred small and large colonies.

had ever had oscula was that the anastomosing tubes converged towards the points where the oscula had been.

These specimens, after being a few days in the aquarium, recovered slowly from their drooping condition, like a plant that has been transplanted. The tubes became rounded and of a healthy appearance, and sent out diverticula, which grew often to 10 or 12 mm. in length, and attached themselves to the side of the vessel. Such diverticula occur in the natural condition also (see fig. 2). From the places where oscula had been breast-shaped eminences raised themselves, which were normal closed oscula like fig. 3. Sometimes a small opening would appear in the "nipple," but only once did I observe in my aquarium that one of my specimens opened out a large normal osculum. Specimens with closed oscula like fig. 3 are of frequent occurrence in nature, and I have often observed them in specimens fished up fresh on the steamer. I went on three separate occasions to the only locality where this sponge occurs abundantly in the Gulf of Naples—a very sheltered grotto near Capo Miseno,—and the following short journal of observations may be of interest:

Oct. 2nd.—A fine bright day, the water smooth and clear. All the specimens had wide open oscula.

Oct. 8th.—The weather as before. All the specimens had open oscula, and on this occasion I preserved fresh from the sea the colony from which figs. 1 and 2 are taken. In one large specimen I observed a closed osculum.

Oct. 19th.—The sea was smooth, but the day was cloudy, and the water in the grotto was turbid, so that when I dived it was difficult to see the sponges clearly under water. There had been scirocco and bad weather previously. Every specimen examined had closed oscula.

Since this date the weather has been so bad and the sea so rough that the steamer has been unable to put out, and so my observations are extremely incomplete; but they give one at least the suspicion that the state of the sea and weather influence the sponge, and cause it to contract or open: and, indeed, one can hardly wonder that it should be so. Leu-

cosolenia clathrus, in the widely expanded condition, is one of the most delicate organisms known to me, the least touch being sufficient to break or tear it. If it is even lifted out of the water the tubes and oscula collapse. In the whole Gulf of Naples it is only known to occur in profusion in one grotto. This is a kind of natural tunnel running through a rock peninsula, and putting a small bay in communication with the sea; but the tunnel runs through obliquely, and meets the shore-line at an angle which is acute towards the open sea: hence the waves can never break into it with much force, and it is exceedingly sheltered. But even here it might well be imagined that the sea would be too rough for this delicate animal. When the sponge is contracted, however, it is very much firmer and stronger, and can be handled with more safety. I noticed that the sponges brought home on Oct. 19th with closed oscula did not droop in the same manner as those brought home on Oct. 2nd and Oct. 8th, but remained healthy and firm. A specimen in a similar contracted condition would be much more able to withstand the force of the sea than one expanded.

It is not, however, only the oscula that can contract, but the tubes can also contract very greatly. In fig. 5 is represented, magnified four diameters, a small piece cut off a specimen which had been growing in my aquarium for a month, and which is still quite healthy. It has fairly attached itself on all sides, and is continuing to send out processes, many of which can be seen in the figure. This sponge, when it first came under my notice, was a specimen like that in figs. 1 and 2. After it recovered from the transplantation it several times completely expanded, and it was in this specimen that I saw the only completely open osculum I have ever seen in the aquarium. The manner in which the sponge had alternate periods of expansion and contraction was noteworthy. It would frequently be widely expanded one day and contracted the next. I could find no cause for these expansions and contractions; only about the last week in October the weather became very much colder, and a chilly tramontana blew for

some days. The sponge contracted completely when the cold weather began, and has not expanded since; but it is still perfectly healthy, as shown both by the histology of sections from portions of it, and by its continuing to grow and send out processes.

If we compare fig. 5 with figs. 1 and 2, it is obvious that the tubes have shrunk to about one eighth of their former diameter. Imagine now a Leucosolenia tube, with its walls composed of ectoderm externally, jelly containing a single layer of spicules and a few cells, and most internally a continuous, closely packed lining of collared cells. If this tube contracts greatly what must be the result? There can be no longer room for the collar cells to form a single layer, and the spicules will also be closely packed, probably into several layers.

Figs. 15 *a* and *c* represent two sections from a series through some partly contracted tubes. The spicules now form at least two layers in the much-thickened mesoderm, and the collar cells are arranged in a stratified epithelium, of which the uppermost only bear flagella. In some places the endoderm is thrown into folds (fig. 15 *c*). In other words, we have before us Haeckel's variety Ascetta mœandrina.

Mr. Bidder, in his recent review of Dendy's 'Monograph of the Victorian Sponges,'[1] has written (p. 628), "In these Australian sponges (Calcarea Homocœla) there appears to occur none with a many-layered endoderm. This structure, observed by Haeckel, and since universally discredited, certainly appears in Ascetta clathrus." I must say that a many-layered endoderm as a normal feature of sponge anatomy is to me as inconceivable as that a sponge should be permanently without an osculum. In every preparation I have made of this sponge in the expanded condition I find a single-layered endoderm. On the other hand, if the sponge be sufficiently contracted, a many-layered endoderm does and must occur. One usually finds it in preparations made from

[1] 'Quart. Journ. Micr. Sci.,' vol. xxxii, part 4, October, 1891, pp. 625—632.

sponges living in the aquarium, and also in freshly preserved sponges which are contracted.

Fig. 14 represents a section taken at random from a series through the piece represented in fig. 5. Here the contraction has reached almost its limit. The spicules form in places as many as five layers (in the section figured the razor has displaced them a little, in a direction passing from the north to the south of the drawing), and the endodermic layer is now so thickened that the lumen of the tubes is reduced to series of narrow lacunæ. In some places the tube is even solid, as Oscar Schmidt described originally. It is evident from Oscar Schmidt's figure of the sponge that he had to do with a very contracted specimen. In almost every respect the sponge agrees with Haeckel's Ascetta clathrina, both in external form and in anatomy. It is true that the compartments (Fächer) are not separated from one another by "exoderm" (i. e. mesoderm), covered on both sides with endoderm; but if a specimen with folded endoderm, as in fig. 15 *b*, were to completely contract, that might be the case. It is true also that the compartments do not contain embryos, but that, I suppose, would depend on the time of year at which the sponge was observed.

Thus, to recapitulate: Haeckel's Ascetta labyrinthus is the ordinary expanded condition of this sponge, but with closed oscula, like the piece shown in fig. 3. His Ascetta mœandrina is the same a little contracted, as in fig. 15. Ascetta clathrina is the sponge in an extreme state of contraction, as in figs. 5 and 14. Finally, Ascetta mirabilis is this sponge partly expanded, partly contracted.

In the walls of the tubes also there are no elements to which the contraction could be due except the ectoderm-cells; and to the great power of contractility I attribute the fact that the ectoderm[1] in this sponge is, as Metschnikoff observed, so

[1] Mr. Bidder has recently described (loc. cit., p. 628) the ectoderm of this sponge as consisting of the mushroom-shaped cells described by Metschnikoff in the Olynthus (Clistolynthus!) form of Ascetta blanca. I do not wish at present to enter into histological details, which I hope to do in another

exceedingly distinct. I find the very greatest difference in this respect between Leucosolenia clathrus and L. coriacea occurring at Plymouth.

To sum up the results obtained:

Leucosolenia clathrus is not permanently lipostomous, but has very large and distinct oscula.

These oscula are provided with a sphincter by which they can be completely closed for a time, apparently as a protection against unfavorable external conditions.

Haeckel's four varieties of the sponge are only different states of contraction, and are no more zoological varieties than a polyp with contracted tentacles is a variety of a polyp with expanded tentacles.

The many-layered endoderm is also only a temporary condition, the mechanical result of the contraction of the whole sponge.

The contractile elements in all cases are the flattened ectodermal epithelium.

In conclusion, it is my pleasant duty to express my thanks to the staff of the Naples Zoological Station, and especially to my kind friend Sig. Cav. Lo Bianco, without whose help this work could never have been done.

Naples; November 10th, 1891.

Addendum.

While the above was in the press, a work by von Lendenfeld has appeared, entitled "Die Spongien der Adria.—I. Die Kalkschwämme" ('Zeitschr. f. wiss. Zool.,' Bd. liii, Heft 2, pp. 185—321, Taf. viii—xv; and Heft. 3, pp. 361—433), containing a detailed account of Ascetta clathrus (pp.

paper, but as my figures might be thought to be erroneous I will only say that in freshly preserved material of the sponge the "Metschnikoff's cells" only occur sparingly, the predominant form of the ectoderm being flattened epithelium; and I have almost conclusive evidence to show that the "flask-shaped cells" are only the contracted condition of the flat cells.

210—217, Taf. viii, fig. 4; ix, figs. 27—37). The author divides the sponge into four forms, which he terms A, B, C, and D, rejecting Haeckel's varieties, "since these forms appear to arise one from the other in the course of the post-embryonal development." Form A consists of a mass of anastomosing tubes, 1—5 mm. in diameter, the walls of which have pores and contain numerous stellate connective-tissue cells, but no large granular elements; the endoderm forms a single layer. In Form B the tubes are only 0·3—1·5 mm. in diameter, and form a flat spread-out creeping network. Pores are rare, and the "zwischenschicht" (mesoglœa) contains, besides stellate cells, large granular, spherical or irregular cells; the endoderm is many-layered. Form C is similar externally to Form B, but has no pores in its walls; the same large granular cells occur as in B, and the endoderm is many-layered but more closely packed than in the latter form. Form D consists of a flat network of trabeculæ, 1·5—3 mm. thick, in which no pores were to be found; in the mesoderm large granular cells were not observed, and the endoderm fills up the interior of the tubes, leaving only irregular lacunes. All the forms agree in having no oscula visible to the naked eye, and are reticulate Auloplegmas. The author believes that the many-layered endoderm and the closing of the pores is connected with the ripening of the eggs (see p. 217). Dr. von Lendenfeld has made a considerable advance in rejecting Haeckel's varieties, but is nevertheless far from a correct explanation of the different forms, which are nothing more than different states of contraction of the sponge. Thus his fig. 30 (Taf. ix), representing a section of Form D, is in all essentials completely similar to my fig. 14, which is taken from a series of sections through the piece of sponge shown in fig. 5. This sponge, as above described, when first collected was like the specimens shown in figs. 1 and 2, and after completely contracting, frequently expanded again to this form. I have recently observed a similar contraction in another sponge, an Ascon of a beautiful orange-red colour, but with the spiculation of Ascetta primordialis, which when

brought in by the fishermen was widely expanded, with large open oscula. In a few hours it contracted completely, the tubes shrinking to perhaps one tenth of their former diameter, and having no visible oscula. The following morning, being placed in a current of pure sea water, it again expanded to its former dimensions and opened its oscula; but the current being stopped, it slowly contracted again. In the evening I again placed it in the circulation, and the next morning it was expanded a third time, though not in all parts, the tubes furthest removed from the oscula being to a certain degree contracted. Some of its oscula opened completely, others were closed and breast-shaped, but at least visible; whereas, in its completely contracted state, it was impossible to see that the sponge had ever had oscula. On the strength of these so oft-repeated observations, I cannot but state my disbelief that any Ascon (or any sponge) is permanently lipostomous; and I have no doubt that where von Lendenfeld has described Auloplegma forms, e. g. in Ascetta spinosa (op. cit., p. 203), he has simply overlooked the oscula, as he has certainly done in Ascetta clathrus. The large granular cells in Forms B and C admit of a very simple explanation; they are simply closed pores, which the author has overlooked in Form D, where they are equally common. Other points of histology I hope to criticise in another place. I will only draw attention to the statement (p. 190), that in sponges the "skeleton forming, sexual, and muscular cells are formed in the mesoderm, and are not of epithelial origin" (compare also the account of the "zwischenschicht," pp. 398—405). After what I have already written, this statement requires no further comment.

Naples; 1st March, 1892.

DESCRIPTION OF PLATE XXIX,

Illustrating Mr. E. A. Minchin's paper on "The Oscula and Anatomy of Leucosolenia clathrus, O. S."

PLATE XXIX.

All the sections of the sphincter have been drawn so that the inner (gastral) face of the sphincter looks towards the south, the outer face towards the north side of the plate.

The following letters are for all the figures.

ect. Ectoderm. *end.* Endoderm. *a. m.* Amœboid mesoderm-cell. *mes.* Jelly (mesoglœa) containing spicules. *s.* The muscular sphincter of the osculum.

Fig. 1.—Two oscula from a large colony, preserved fresh from the sea in 70 per cent. alcohol, in profile view. One of them (*a*) is widely open, the other (*b*) half closed. Natural size.

Fig. 2.—Three more oscula from the same colony viewed from above. Natural size.

Fig. 2 *a*.—The osculum of Fig. 2 viewed as a transparent object, magnified about three diameters. It is very slightly contracted.

Fig. 3.—A closed osculum. Natural size.

Fig. 4.—A small colony with three oscula, magnified five diameters.

Fig. 5.—A piece of a colony in a very retracted condition, the Clathrina clathrus of Oscar Schmidt, the Ascetta clathrina of Haeckel.

Figs. 6 *a*, *b*, *c*, *d*.—Four sections from a series through one of the oscula of the colony represented in Fig. 4: 6 *a*, a section near the middle of the series; 6 *b*, the next section after 6 *a*; 6 *c*, the next section but one after 6 *b*; 6 *d*, the thirteenth section after 6 *a*. Magnified 350 times. Osmic half per cent., picro-carmine, hæmatoxylin.

Figs. 7 *a* and *b*.—Two sections from a series through a large expanded osculum like those in Figs. 1 and 2: 7 *a*, a median section; 7 *b*, a thick tangential section. × 330. Abs. subl., borax carmine, hæmatoxylin.

Fig. 8.—A median (transverse) section of the sphincter of another large open osculum. Osmic half per cent., picro-carmine, hæmatoxylin. × 330.

Figs. 9 *a*, *b*, *c*.—Sections from a series through the closed osculum in Fig. 3: 9 *a* and *c*, tangential section; 9 *c*, a detached muscle-cell. Abs. subl., borax carmine, hæmatoxylin. × 330. (In one place the section 9 *a* is slightly broken.)

Fig. 10.—Nuclei from a series of sections through the sphincter of an expanded large osculum. Hermann's fluid, safranin, gentian violet, orange G. Zeiss, compens. ocular 8, apochr. F.

Fig. 11.—Surface view of a relaxed sphincter of the osculum of a large colony. One third alcohol, picro-carmine, glycerine preparation. × 500.

Fig. 12.—Surface view of another similar preparation. × 500. 12 *a*, an isolated cell from this preparation. The upper (north) limit of Fig. 12 represents the natural free edge of the sphincter.

Figs. 13 *a* and *b*.—Two views of another preparation similar to that from which Figs. 11 and 12 are drawn: 13 *a*, drawn with the microscope at the lower focus; 13 *b*, with the upper focus. × 430.

Fig. 14.—Section from a series through the piece of sponge represented in Fig. 5. × 70. Abs. subl., borax carmine, hæmatoxylin.

Figs. 15 *a*, *b*, *c*.—Sections from a series through a contracted sponge. 15 *b* is a portion of 15 *a* more highly magnified to show the many-layered endoderm. Abs. subl., borax carmine, hæmatoxylin. 15 *a* and *c* × 120.

Fig. 1.

Fig. 2.

Fig. 2,a.

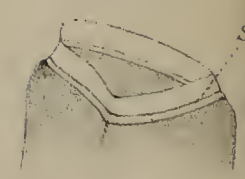

Fig.

Fig. 7,b.

Fig. 12,a.

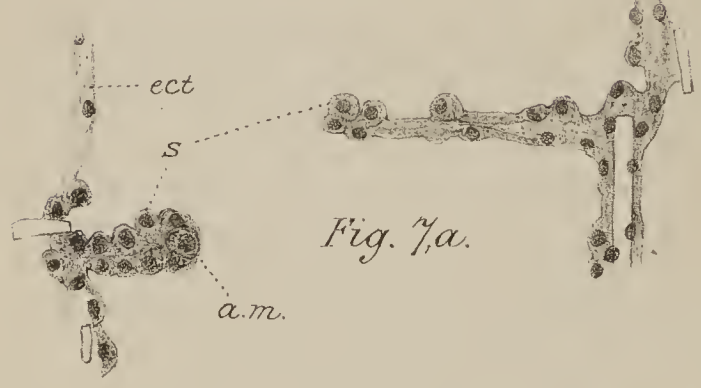

Fig. 7,a.

Fig. 12.

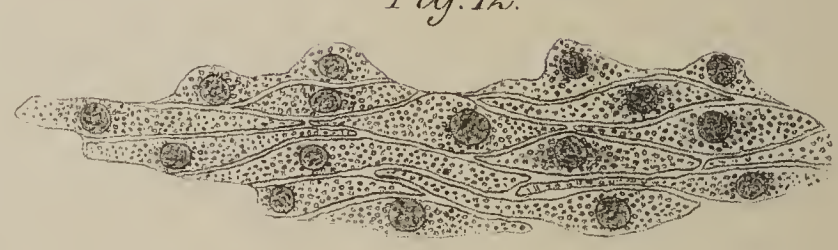

Fig.

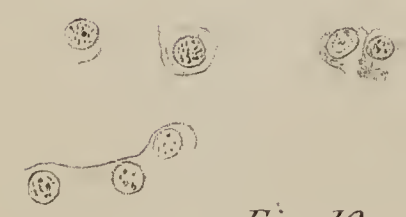

Fig. 10.

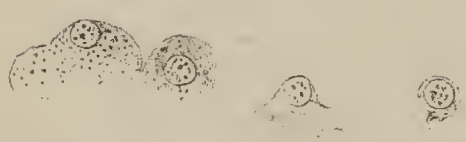

Fig. 11.

Fig. 14.

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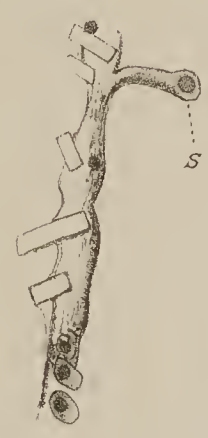
Fig. 4.
× 5

Fig. 5.
× 4

Fig. 6,b.



9,c.

Fig. 9,b.

a.

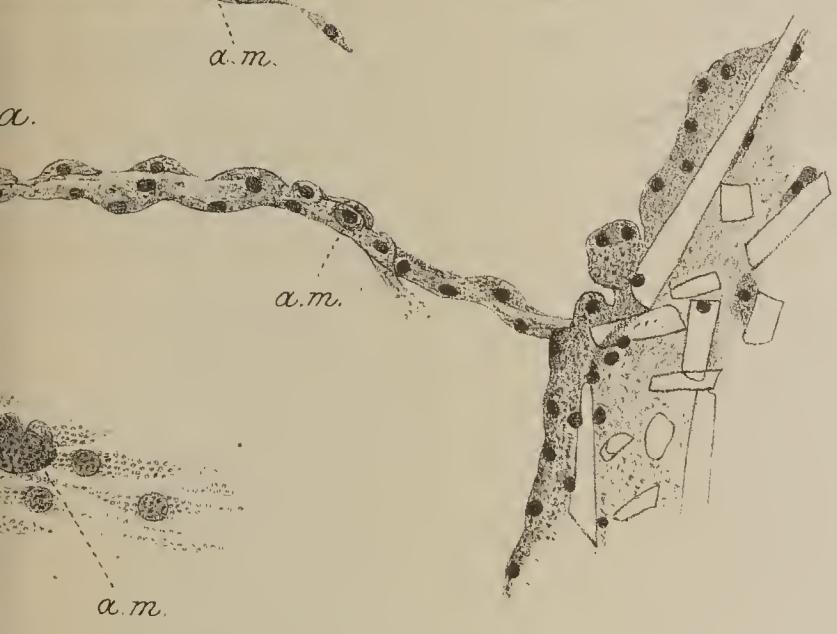


Fig. 6,c.

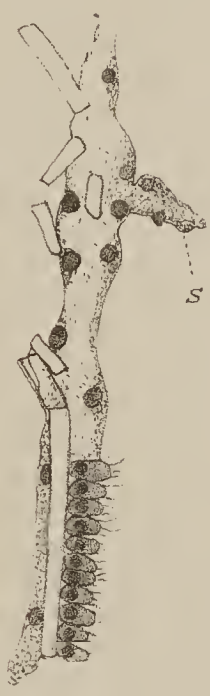


Fig. 15,a.

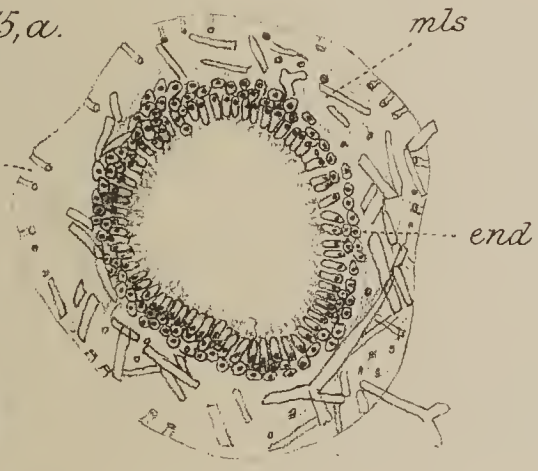
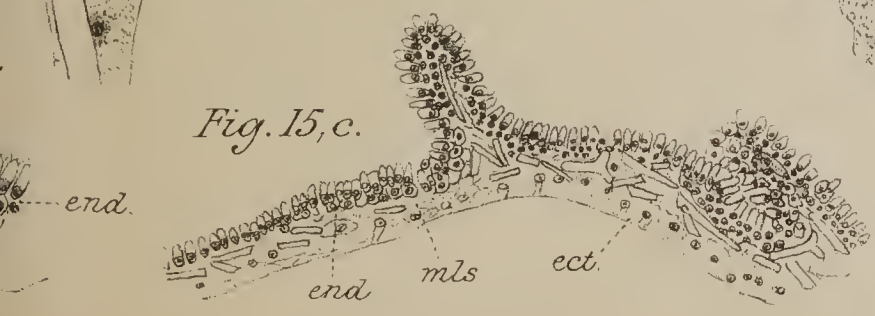


Fig. 6,d.

Fig. 6,a.

Fig. 15,c.



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Observations on the Gregarines of Holothurians.

By

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With Plates XXVII & XXVIII.

Our first knowledge of the Gregarines of Holothurians dates back to Kölliker (1), who in 1858 described "vesicles for the most part stalked, with a distinct envelope, and granular, dark, fat-like contents, which invariably contained two germinal vesicle-like bodies, each with a large, finely granulated, germinal spot-like structure. Some of these structures were sessile on the (blood-) vessels (of the intestine and respiratory trees), and were covered by ciliated peritoneal epithelium, while the stalked ones were apparently always naked." The author was at a loss to understand the significance of these structures, and "simply recommends them to later observers."

In the following year Anton Schneider (2) identified these bodies as Gregarines, and termed them Gregarina holothuriæ. He found them in the intestine, blood-vessels, and free in the body-cavity, and figures a specimen from the blood-vessels, where by continually increased bulging out of the wall they form the stalked vesicles of Kölliker. In all those from the blood-vessels he observed two nuclei, as also in many from the body-cavity. In the latter by slight pressure of the cover-glass he observed a furrow dividing the contents into two halves, each with a nucleus; in the former he could not observe this furrow. In contradiction to Kölliker he found

even the stalked vesicles ciliated, but since they finally fall off into the body-cavity he thinks that at a certain period they would cease to be ciliated.

The author further figures the mature psorosperm, and identifies as a stage in the evolution of the Gregarine certain amœbæ forming the chief mass of the brown bodies. They are homogeneous, without nucleus, and of fat-like contours. For the most part they move slowly or are motionless. A gradation of size could be found in these amœbæ up to bodies as large as the smallest or middling-sized Gregarines.

In 1861, Sars (**3**, pl. xvi, figs. 2—7) figured Gregarine-like bodies from the gut of Chiridota pellucida (= C. lævis). Since this date no further works dealing specially with these organisms have, to my knowledge, appeared until the year 1891, when Cuénot (**4**) and Mingazzini (**5**) published researches upon the Gregarines of Holothurians quite independently of one another. Ludwig (**10**) also gave an account of the parasites of Holothurians, together with a complete literature of the subject.

Cuénot (**14**) places the Gregarines of Holothurians in the genus Syncystis, Aimé Schneider, and describes three species, Syncystis synaptæ, E. R. L., sp., from the cœlom of Synapta inhærens, S. holothuriæ, Ant. Schneider, sp., from Holothuria tubulosa, and S. Mülleri, Giard, sp., from the cœlom of Synapta digitata. Mingazzini (**5**), on the other hand, places these Gregarines in the family Syncystidæ, but erects for them a special genus Cystobia, of which he describes two species, Cystobia holothuriæ, Ant. Sch., sp., and C. Schneideri, n. sp., from Holothuria Poli and impatiens. Further details in these authors' works we shall refer to below under the special descriptions of these Gregarines.[1]

[1] It should be mentioned that in 1852 Leydig described "dark planarian-like bodies, with egg-like structures embedded in them," and vesicles containing pseudo-navicellæ floating free in the body-cavity of Synapta digitata ('Archiv f. Anat. u. Physiol.,' 1852, in "Anatomische Notizen über Synapta digitata," pp. 517, 518, Taf. xiii, fig. 11).

My own acquaintance with these interesting parasites began in the year 1889, when as a student in the Oxford Laboratory I found a specimen of Holothuria tubulosa, from Naples, supplied for dissection, with its body-cavity filled with cysts, some containing sporoblasts, others ripe psorosperms or spores. Having investigated these cysts and their contents, and written a short description of them, I forwarded the description with some material to Professor Bütschli, of Heidelberg, whose pupil I had had the honour and pleasure to be for a short time during the previous summer. Professor Bütschli with characteristic kindness examined the material, and in a letter accompanied by a sketch pointed out to me that I had overlooked the most important points, viz. the formation of the sporozoites within the spore. I determined, therefore, before publishing anything, to examine fresh material, which I was fortunately able to do both at Plymouth in the summer of 1890, when as the occupant of a British Association table I studied the Gregarines of Holothuria nigra, and at Naples, during my occupation of the Oxford table there in 1891–2. The results of my investigations on the two closely allied gregarines found in these Holothurians are far from complete, but it seemed to me better to publish them in their present crude form than to wait, perhaps, some years before I can complete them. Like Kölliker, I would simply recommend these interesting forms to later observers, who will, I hope, fill up the gaps in the following description.

I shall begin with the description of the Gregarine of Holothuria nigra, in which my series of stages is most complete. This Holothurian occurs commonly at Plymouth, and can be obtained in numbers. The dissection of the animal is not without its difficulties, both on account of the large number of Cuvierian organs it emits, and by reason of the force with which its powerful body muscles contract on the least stimulation, thereby much impeding the examination of the fresh contents of the body-cavity. In the majority of the specimens of Holothuria nigra observed by me the blood-vessels could be seen to bear little stalked vesicles, which on exami-

nation were found to contain spores, sporoblasts, or (in one instance) sporoblasts together with nucleated protoplasmic masses of various sizes. Only in a single instance did I succeed in finding the adult Gregarine. In this instance the blood-vessels, which are of a rich brown colour, bore no vesicles, but a few opaque white spots could be plainly observed in the interior of the vessels, shining through the dark walls. The walls of the vessels were not evaginated in any way, and by gently pressing the wall of the vessels these white spots, which were the adult Gregarines, could be made to shift their position. By snipping the blood-vessel with scissors close to the white spot and pressing it, the Gregarine was made to emerge quite uninjured from the cut end. Examination with the microscope showed an opaque white mass, appearing black of course in transmitted light, quite motionless, of irregular shape (fig. 1), and of such strange appearance that at first I doubted if it was a Gregarine at all, the more so as even after fixing and staining, and clearing the object in oil of cloves, I could observe nothing of a nucleus or other structure, so great was the opacity of the protoplasm. By careful searching I found four more Gregarines, making five in all. Of these five, two were stained and mounted whole in Canada balsam, a third was teased up in order to try and find the nucleus (this preparation proved, however, useless), while the remaining two were carefully removed without disturbing them in the blood-vessel, fixed with Kleinenberg's picric, and cut into a series of sections.

Fig. 1 shows one of these Gregarines drawn living when freshly removed from the Holothurian. I have the same specimen now mounted in Canada balsam, but it is so opaque and granular that I can make out no more of the structure than is shown in the figure ; the nuclei, which were probably faintly stained, escape observation even with the most careful focussing. Fig. 2 represents another animal, drawn from a Canada balsam preparation, in which eight faintly stained nuclei can be plainly made out, and have been drawn with the camera in their natural positions. In addition a faint but dis-

tinct septum could be discerned, dividing the animal in two. This is probably an early stage in the encystation which we shall discuss later.

The best results were given by the two Gregarines which were cut into sections, and which I shall denote as A and B respectively. A was cut into sections of about 10μ in thickness, B into sections of about 5—7μ. In A the relations of the parts to one another were best shown, while B showed better minute structure, the relations of the parts to one another being often distorted. To begin with A: the entire Gregarine ran through exactly forty sections. In the 14th section from one end a nucleus makes its appearance, which runs through five sections, disappearing after the 19th section. Fig. 3 represents the 15th section, showing the blood-vessel with the Gregarine in the interior × 128. Fig. 4 is the interior part of the same section × 315. The 20th to the 30th sections contain nothing special. At the 31st section another nucleus makes its appearance, disappearing after the 35th section. Figs. 5, 6, and 7 represent the 34th, 33rd, and 31st sections respectively. The last five sections contain nothing special. It is thus evident that this Gregarine contains two large nuclei, each running through five sections 10 μ in thickness. Similar results are given by B, which runs through ninety-six sections. The first nucleus appears at the 10th section, runs through eight sections, and disappears after the 17th. The second nucleus appears at the 78th section and vanishes after the 85th. Fig. 8 represents the inner part of the 80th section × 315, while 8 *a* represents the nucleus only, from the same section, ×730.

To proceed now to study the finer structure of these animals.

The body is limited by a distinct cuticle, appearing as a sharp single contoured line, best seen in fig. 8, where the Gregarine is not in contact on one side with the blood-vessel. The protoplasm of the body is very opaque, and filled with coarse granules of various sizes. No distinction could be found between an ectosarc and endosarc.

The nuclei are very large, each surrounded by a clear space. In sections this space appears filled by a finely granular or streaky coagulum (fig. 7). It sometimes appears as if the nucleus were suspended in this place by threads (fig. 6), but I think this appearance is only due to coagulation of the fluid, probably albuminous, which filled these spaces during life. The nucleus itself is about 50 μ in diameter, and surrounded by a strong nuclear membrane, which usually appears wavy in section, owing, doubtless, to shrinkage. It has a single large nucleolus about 25 μ in diameter, the remaining space of the nucleus being filled with cloudy or very finely granular contents, with a number of darker spots. At first it seemed as if these dark spots might represent the nodes of a fine reticulum supporting the nucleus, but I was unable to detect any such reticulum with the Homogen. Immers. 2·0 mm. of Zeiss (fig. 8 *a*), and the nucleus appeared to be filled with a fine coagulum, but of a different nature from that filling the clear space surrounding it. It is possible, or even probable, that the nucleolus is kept in place by fine strands of chromatin or other substance fastening it to the nuclear membrane, without, however, any definite reticulum.

The nucleolus itself deserves particular description on account of its peculiar structure. In the sections through A it appeared as a round spot, very darkly stained (with hæmatoxylin), containing a lighter vacuole-like spot somewhat excentrically placed. Examination of the thin sections through B made clear the real structure of the nucleolus (figs. 8, 8 *a*). It consists of a darkly stained ground substance containing an immense number of clear vacuoles of all sizes. One of the vacuoles is much larger than the others, and being excentrically placed, constitutes the clear spot seen in the thick sections. Some are excessively minute, and almost escape detection. In fig. 8 *a* the minute vacuoles can be seen in the obliquely cut wall of the large vacuole, producing an appearance which under lower magnification looks like a network.

The darkly staining ground substance of the nucleolus should, after the analogy with the cell nuclei of higher animals,

be chromatin, and the clear unstained vacuoles achromatin; but it would be unsafe to identify the two constituent parts of the nucleolus as such simply from their reaction to stains. With all due caution, however, a comparison may be made with, for instance, the results obtained by Pictet (8) in studying the spermatogenesis of Echinoids, where the achromatic portion of the nucleus of the spermatocyte separates out to form a number of vacuoles or "cytomicrosomes," which fuse together to form the single "Nebenkern." I am not aware that a nucleus of similar structure has as yet been described, though it is an old observation that the nucleoli of Gregarines often contain vacuoles (see Bütschli, 6, p. 525). Wolters (9), in his valuable studies on the conjugation and spore formation of Gregarines, describes the nucleolus of Clepsidrina blattarum as containing "more strongly stained spherules of varying size and shape" (p. 118): the nucleolus of Monocystis agilis is similarly described (p. 106). Schneider ('Tablettes zoologiques,' i, pl. vi, fig. 9) figures the nucleus of Pileocephalus chinensis, containing numerous spherical nucleoli, some dark, others light. The vacuolar structure of the nucleolus in the Gregarine seems to me to support strongly Professor Bütschli's theory of the frothy structure of protoplasm.

The greater number of Holothurians examined had, as has been said above, stalked vesicles attached to the blood-vessels which contained cysts. Some of these cysts I teased up and examined the isolated spores, while others I cut into sections. As it turned out I was not particularly lucky in my selection, for the only cysts which were found to contain perfectly mature spores were the very ones I had selected for sections; while among those teased up one was found to contain, besides sporoblasts, large nucleated masses of protoplasm, the relation of which to the sporoblasts it was of course impossible to ascertain by this method.

Fig. 10 represents one of these cysts attached to the blood-vessels, and fig. 9 shows another, which had an exceptionally long stalk; 9 *a* represents a portion of the edge of the same cyst in optical section.

The cysts are covered by a layer of flattened epithelium which also forms the hollow stalk, and is continuous with the peritoneal epithelium covering the blood-vessels. This is best seen in section (fig. 15 *a*). The wall of the cyst proper is formed by an external very thin jelly-like layer, which cannot be plainly seen in sections, and internally to this a strong structureless membrane, appearing in section as a double contoured line (fig. 15). The cysts themselves are exceedingly opaque, and nothing can be learnt as to their contents without further preparation. They are quite spherical, and have no ornamentation of any kind.

In the sporulation I have observed three stages:

1. The sporoblasts (fig. 11, *a*, *b*, *c*). Many cysts occur filled with little spherical nucleated masses of protoplasm. In the living condition (11, *a*) they are filled with strongly refringent granules, the central nucleus appearing as a faint clear space. They are surrounded by a double contoured membrane. After fixing and staining (fig. 11, *b*, *c*) the nucleus is distinct in many of them, but they do not stain easily, perhaps on account of the thick cell-wall. When visible the nucleus can be seen to have irregular aggregations of darker stained substance round the edge, and to be lighter towards the centre. These bodies are the final results of the segmentation of the protoplasm within the cyst, or the sporoblasts. They also occur singly in cysts containing spores, which is probably due to arrested development. In one cyst I found, besides great numbers of sporoblasts, a few nucleated masses of protoplasm of various sizes containing one to three nuclei (fig. 11, *d*, *f*) which were much larger than the nuclei of the sporoblasts. Their structure was difficult to make out on account of the opacity of the protoplasm, but in one instance a nucleus could be seen to contain vacuoles (fig. 11, *f*), and two other nuclei were found isolated and had a vacuolar structure (fig. 11, *c*), recalling the nuclei of the adult Gregarine. The exact relations of these masses of protoplasm could not be made out with the method employed, and it was only certain that they were

placed more in the interior of the cyst, and the sporoblasts more peripherally.

2. The stage found most commonly[1] was that of spores each containing four nuclei (figs. 12, 13). In this stage the cyst is completely filled with spores, and with the exception of a few sporoblasts occurring sparsely there is no unused protoplasm. The spores are egg-shaped, one end broader than the other. At the narrow end the membrane of the spore is continued into a well-marked funnel, the lumen of which is, however, shut off from the contents of the spore by a delicate diaphragm. The cuticle is composed of two distinct layers, an inner thicker one and an outer thinner one. Both layers appear to unite to compose the funnel, which is formed of a single contoured thin cuticle, but the diaphragm closing the mouth of the spore is probably derived from the inner layer only. These structures are best seen after treatment with a 10 per cent. solution of sodium carbonate, which clears the contents of the spore (fig. 14). In some spores the diaphragm lies close upon the spore contents (fig. 14, *b*), in others it is raised up from them and bulges into the funnel (fig. 14, *a*).

The spores contain four spherical nuclei (which, however, like the nuclei of the sporoblasts, are often not stained in preparations). The nuclei have a distinct membrane, and if carefully examined with a high power in a favorable preparation can be seen to have the chromatin substance aggregated round the periphery, being clear centrally. They are usually arranged more or less regularly in the angles of a rectangle, two being near the broad end and two near the narrow; but variations from this arrangement are common. In one instance a spore was found to have three nuclei (fig. 13, *c*); two of the ordinary size and appearance near the narrow end, and one larger nucleus placed close to the broad end, and distinctly elongated transversely to the long axis of the spore, as if about to divide. From this it may be reasonably inferred that the two pairs of nuclei placed at the narrow and the broad end respectively are each the product of the division of a single nucleus, so that

[1] These observations were made in the month of July.

in an earlier stage there was one nucleus at each end of the spore. Further, since these two nuclei must be derived from the single nucleus of the sporoblast, we may piece together the following history. Either before or after the assumption by the sporoblast of the elongated shape of the spore, its nucleus divides in two, the two halves going to opposite ends of the spore. The two nuclei thus produced then each divide again into two in a plane at right angles to their former plane of division, so that we get the stage here described with four nuclei, the protoplasm of the spore having in the meanwhile secreted the cuticle and its appendages. It may be pointed out in passing how much larger the nucleus of the sporoblast is than that of the spore.

3. Ripe spores were found in four cysts which were removed attached to a blood-vessel and cut into sections (figs. 15, 16, 17, and 18). The external form of the spore and the structure and arrangement of its cuticle are the same as in the last stage; but each spore now contains instead of four nuclei eight sporozoites[1] (falciform bodies). It is a little difficult in studying the sections to be certain of the exact number, since a spore might often be halved or partially removed, leaving only a few of the sporozoites. Nevertheless, wherever an uninjured spore could be satisfactorily observed, eight sporozoites could be plainly made out, and in very many cases where a spore was cut transversely eight sporozoites could be seen (fig. 16, *b*); and it may, I think, be taken as certain that this is the full and normal number in each spore.

The sporozoites are exceedingly minute, and by no means easy to make out. Nevertheless careful focussing with a Zeiss's oil immersion 2·0 mm. showed them to consist of an elongated darkly staining nucleus forming the head, to which is attached at one end a delicate flame-like tail, doubtless vibratile, and at the other end, which we may term anterior, a minute conical point; but the latter structure was exceedingly

[1] Wolters uses the term "sporocysts" for what are here termed spores, and "spores" for what I have used the name sporozoites. I have kept to the nomenclature of Bütschli and Schneider.

difficult to be certain of. Their typical arrangement appears to be in two rows of four, with the nucleus towards the narrow or infundibular end of the spore, and the tail pointing away from it. Nevertheless variations occur constantly from this position, one or more of the sporozoites being turned round with the tail towards the spore-funnel. The thin diaphragm at the base of the funnel is probably the spot at which the spore-wall breaks to liberate the sporozoites, and the more or less constant position of the latter, with their heads turned towards the funnel, doubtless is in connection with this fact. It is probable that the sporozoites are motile within the spore, which would account for their not unfrequent reversal of position.

They very often appear closely applied to the wall of the spore. Since the tails of the front row overlap the heads of the hinder row, we can understand how it is that all the eight are to be seen in section. They lie embedded in the granular mass or "nucleus de réliquat" (sporophore—Wolters) filling the spore, which doubtless serves as nourishment for the growing sporozoites. If we compare fig. 15, *b*, or 16, *a*, with fig. 13, *c—g*, which are drawn to the same scale, it is evident that the bulk of the nucleus of a sporozoite is about half that of a nucleus of a spore in the last stage, and it is scarcely to be doubted that each nucleus in the stage with four nuclei has divided in two to furnish two sporozoite nuclei, which elongate to form the "head" of the sporozoite, while protoplasm becomes aggregated round them to form the tail. In the four cysts which I cut into sections I was able to find two stages of the sporozoite. The first is shown in fig. 16 : *a* represents a spore in which six sporozoites could be seen ; *b* and *c* show two other spores, one showing five sporozoites, the other in transverse section showing eight, both magnified about 1000 ; *d*, *e*, and *f* show three sporozoites much more magnified. In this stage the nucleus is not more than twice as long as broad, and the tail is short and stumpy. The second stage, and probably the final one, is shown in figs. 15 and 17, and in fig. 18, which is a combined semi-diagrammatic figure. The nucleus

is now four or five times as long as broad, and the tail longer still. Both nucleus and tail are often slightly flexed, especially when the sporozoite lies close along the side of the spore. Both in this stage and the last the nucleus does not stain evenly, but more darkly in some parts than others.

There remains now only to be considered the Gregarine represented in fig. 2. This is seen to be separated into two halves by a septum, in each of which are four nuclei. I was at first inclined to consider the septum as produced by the fusion of two animals, but am now more inclined to consider, for reasons which will be set forth below, the ordinary binucleated adult form as itself produced by the fusion in early life of two separate individuals. In this case it is more probable that the form shown in fig. 2 is the commencement of segmentation in an animal that is about to encyst and form sporoblasts, and that the septum separates what we may term the first two sporoblastomeres. No enveloping cyst-membrane was to be seen in this specimen, but that might have been torn off in removing it from the blood-vessel.

It would be extremely interesting to follow the first stages of segmentation in the encystment of this form. By the analogy of what Wolters (9) has observed in Monocystis magna and agilis it is to be supposed each nucleus would give off a polar body. Only by the observation of this process could the meaning of the vacuolar structure of the nucleolus be properly understood. After formation of the cyst the enclosed animal segments into sporoblasts, which are formed, in a method yet to be described, first at the periphery. While this process is going on the wall of the blood-vessel becomes evaginated to form the stalked vesicle containing the cyst. What causes this evagination it is difficult to understand. It must be due to active growth on the part of the tissues of the host, brought on, however, in some way by the parasite. In Holothuria tubulosa we shall see that the evagination takes place at an earlier stage in the life of the Gregarine than in H. nigra.

To recapitulate, the following are the characters, as far as

I have been able to make them out, of this Gregarine, for which, on account of the irregular form of the adult, I propose the name—

Gregarina irregularis, n. sp.

Gregarines of relatively large size (about ·5 mm. in length) and of extremely irregular form. The body consists of opaque coarsely granular protoplasm, limited by a distinct cuticle, and containing two large nuclei, each floating separately in a clear space free from granules. The nucleus has a distinct membrane and a single large nucleolus of peculiar vacuolated structure floating in a nuclear fluid. After encystment the protoplasm segments and is entirely used up to form spherical sporoblasts, each of which develops into an egg-shaped spore with a funnel-like expansion of the cuticle at the narrow end. The nucleus of the sporoblasts divides into eight nuclei, which elongate and acquire at one end a flame-like tail, at the other end (?) a minute conical point. Thus are formed the eight sporozoites, which are embedded in a coarsely granular "noyau de réliquat," and are typically arranged in two rows of four, the tail of each sporozoite being parallel to the long axis of the spore and pointing away from the infundibular end of the spore.

Habitat.—Blood-vessels of Holothuria at Plymouth. The adult form lies free in the lumens of the blood-vessels, but the cysts evaginate the wall of the vessel to form a stalked vesicle.

We shall now consider the Gregarine of Holothuria tubulosa, the Gregarinæ holothuriæ of Anton Schneider. In the specimens of H. tubulosa examined by me at Naples I found the adult binucleated form occurring as little stalked vesicles attached to the blood-vessels, often in great abundance. In one specimen in particular there must have been thousands, mostly attached to the dorsal blood-vessel of the intestine, and easily seen with the naked eye. In fig. 19 I have represented some of the vesicles as they appeared in the

fresh condition under low magnification, and in fig. 20 I have shown a single vesicle stained and mounted in Canada balsam, with the contanied Gregarine. The animal is egg-shaped or nearly spherical, with two distinct nuclei, and no trace of any septum visible, either in preparations in toto or in section (fig. 21).

The form under which I have found this animal agrees, therefore, with the description given by Kölliker (1). Schneider (2) found it not only in the blood-vessels, but also in the intestine and cœlom. Mingazzini (5), however, seems to consider the water-vascular system ("vasi acquiferi") as the home of this Gregarine. He states that it was first found by Kölliker in the water-vessels and intestine, which, however, is not the case. Kölliker's words, "An den Darm- und Lungengefässen der Holothuria," leave no doubt as to his meaning. At first I thought that Mingazzini must mean blood-vessels by the words "vasi acquiferi," till I found that he terms blood-vessels of Holothurians "vasi sanguigni" or "lacune connettivali," in which he incidentally mentions the occurrence of this form in the following words:—"A peculiar property of this species is the production of special cysts, which are formed in the water-vessels ('vasi acquiferi') when it is present. Nothing of like kind occurs when it is found in the connective lacunes of the intestine" (p. 314). If by cysts ("cisti") the author means the stalked vesicles in which this form is found, he is certainly in error in saying they do not occur on the blood-vessels, which are, in fact, their chief seat, as described by Kölliker and Schneider. For my part, I am inclined to doubt the occurrence of this form in the water-vascular system at all. Mingazzini further states that he has found them free in the body-cavity. Those in the connective lacunes of the intestine have more or less irregular contours. With Schneider he describes the vesicles as detaching themselves and falling into the cœlom when they are ripe for sporification. Up to the commencement of sporification he finds the animal divided in two by a septum. Schneider (2), on the other hand, only found a septum in some of the speci-

mens floating free in the body-cavity, and could observe none in those still attached to the blood-vessels. My observations agree completely with SCHNEIDER, as I never could observe any septum in the specimens still attached to the blood-vessel. On the other hand, since sporulation certainly takes place in the body-cavity, it is probable that the septum seen by SCHNEIDER was that dividing the first two sporoblastomeres, as I have termed them above.

If we sum up the above somewhat conflicting evidence, the following seems to me the most probable history of this parasite. The adult form inhabits the blood-vessels of Holothuria tubulosa, probably coming there from the intestine. As it grows in size it evaginates the walls of the vessels, and hangs into the cœlom. When it is ripe and ready for sporulation the vesicle breaks off and drops into the cœlom, and sporulation then takes place.

To return now to our specimens. Like Gregarina irregularis, this form has a distinct cuticle singly contoured. In sections it seemed to me that I could distinguish an outer zone of protoplasm marked off from that more internal, which I have represented in fig. 23, *a*. The granules in the outer zone are more regularly and evenly arranged than in the inner part, and appear also more of a size. If this differentiation, however, can be compared with what is known as ectosarc and endosarc in other forms is very doubtful. The nuclei are placed in a clear space, relatively larger than in G. irregularis. In its general characters the nucleus resembles that of G. irregularis. It has a distinct membrane, generally somewhat shrunk in preparations made with Kleinenberg's picric, but retaining its even round contour after Flemming's fluid. The nucleus contains a large space, which often appears very granular; but I have never been able, with the highest power, to see the "delicate reticulum" described by MINGAZZINI (5, p. 315). The nucleolus has the same vacuolar structure as that described above, but not quite so well marked, and there is not always a vacuole specially marked out by its size.[1]

[1] This seems to me the proper place to notice the recent work of FRENZEL

In none of the Holothurians studied by me at Naples was I so fortunate as to find any cysts. Other work prevented me from giving as much time to these interesting organisms as I could have wished. I have, therefore, only the material to go upon which I found in the specimen of Holothuria tubulosa from Naples, supplied for dissection at Oxford. In this specimen the body-cavity contained numerous spherical cysts floating free in the body-cavity, each containing an opaque central spherical mass, usually placed slightly excentrically. The diameter of the cysts varied from about 640 μ to 820 μ, and the diameter of the internal opaque sphere from about 550 μ to 590 μ. The difference between these two measurements gives the thickness of the jelly envelope. I found in all cases the cysts perfectly smooth, and am astonished that Mingazzini (5, 314) gives a characteristic of the genus that the wall of the cyst is covered with little spines. I have observed

Joh., "Ueber einige Argentinische Gregarinen, &c." ('Jena. Zeitschr. f. Naturwiss.,' xxvii, pp. 233—336, Taf. viii), which only came into my hands after my paper was finished. The memoir in question, which describes five new Polycystids from Argentine hosts, being mostly filled with details of the microchemical analysis of these animals, contains little which I need notice here with the exception of the peculiar structure of the nuclei in some of the forms. In Gregarina statiræ, G. bergi, G. panchloræ, and the young form of Pyxinia crystalligera, the nucleus is described as possessing a peculiar nucleolus, which the author terms a "morulite." This body is described in G. statiræ as "having a peculiar dull shine [eigentümlich trübe glänzend] with a feebly yellowish light, and being in addition rough, with warty wrinkles on the surface just as in many other Protozoa, and especially Rhizopoda (amœbæ), on which account it is usually termed mulberry-like." It reacts like nuclein, but is specialised to resist digestion, and hence its substance may be termed "morulin" (p. 270).

It seemed to me at first that this might be a vacuolar nucleolus, like those in my Gregarines; but as this could only be made out by very thin sections, a method which Frenzel does not seem to have practised, this point cannot be determined.

By treatment with concentrated acetic acid a delicate wide-meshed network arises in the nucleus, which before appeared homogeneous. In strong nitric acid the morulite slowly vanishes, and only the network is left. It seems to me not impossible that this network is an artificial coagulation of the "Kernsaft."

nothing of the sort either in Gregarina irregularis or Holothuria, and am inclined to think that what MINGAZZINI took for spines were little bits of dirt (bacteria?) sticking to the cyst, as commonly occurs. Nor have I observed anything like the sporoduct described by MINGAZZINI, though it is quite possible that a structure of this kind is formed later. The internal cavity of the cyst is limited by a strong and distinct membrane.

All the cysts which I observed contained either spores or sporoblasts. It was noteworthy that in the latter case the cysts could be recognised by their contents being more or less shrunk by the action of the alcohol, while in cysts containing spores the inner mass was perfectly spherical.

In the case of the sporoblasts, what I have described above for G. irregularis is perfectly applicable here; they are spherical bodies with a distinct membrane filled with strongly refringent granules, and containing an internal nucleus appearing as a clear space, as MINGAZZINI has already described (p. 316).

Fig. 24 represents a spore in outline × 730, and fig. 25, *a* and *b*, two others with the contents drawn in, from a preparation of Professor Bütschli. It can be seen that the spores agree closely in the majority of details with those of G. irregularis. Like them they are egg-shaped, and have a funnel-like expansion of the cuticle at the narrow end. The cuticle has a delicate external layer and a thick internal one, which stains more readily, as Professor Bütschli first pointed out to me. Both layers take part in the formation of the funnel, at the base of which a thin diaphragm is formed by the internal layer. But at first sight these spores appear to differ strongly from those of G. irregularis in the fact that the external layer of the cuticle is prolonged into a delicate caudal process—as we may call it—at the broad end, which is nearly as long as the spore itself. The caudal process is simply a flattened sheet-like extension of the cuticle ending in a point. At its edges it appears to be continuous with two ridges, which run forwards along one surface of the spore to the funnel, curving inwards

slightly towards one another about the middle of their course. Whether these ridges are natural, or are the result of shrinkage from the action of the spirit, I cannot say. The caudal process appears to be broader in its distal half than at its origin, but this is obviously an optical effect due to the caudal process being curled up at the sides and concave on one face.

Schneider (2), who first saw these spores, described them as having two caudal processes instead of one. Mingazzini (5) in his description follows Schneider, but it would appear that he has simply copied Schneider in his description of the spores, and does not describe what he has seen himself. I have examined a very large number of spores from different cysts, and have never observed anything but a single caudal process. Moreover, since the process is extremely delicate, and is slightly curved at the edges, which would hence appear thicker in optical section, it would be easy in a bad light to have the appearance of two processes instead of one. I am more inclined to adopt this explanation of the difference between my observations and those of Schneider and Mingazzini than to suppose that so great a difference could occur in the spores of the same species.

In none of the spores which I examined could I see anything but a confused granular mass in the interior. But in the material which I sent to Professor Bütschli he was able, after staining with hæmatoxylin, to see and draw eight sporozoites. After this I carefully re-examined my material and stained spores in different ways, both with Delafield's and Kleinenberg's hæmatoxylin, but still was unable to get anything stained in the interior of the spores. I wrote, therefore, to Professor Bütschli to ask his leave to reproduce the sketch he sent me, whereupon he most kindly sent me his beautiful preparation of the spores, in which I was able to make out easily all the details described by him in his letter. I am inclined to think that the cyst examined by Professor Bütschli was one exceptionally well preserved; perhaps from greater proximity to the anus, or some other cause, the alcohol in which the Holothurian was preserved reached it quicker and fixed it in

good condition. However that may be, it can be seen from fig. 25, *a* and *b* (drawn from Professor Bütschli's preparation), that the spore contains eight sporozoites, each with a nucleus and flame-like tail embedded in a granular "nucleus de réliquat." Like those described above, they are typically arranged in two rows of four each, with the tail pointing away from the spore funnel, some of the sporozoites, however, being often displaced in position. They differ slightly in details from the sporozoites of G. irregularis, but are perhaps not quite so mature; the nucleus is spherical, and the shape of the whole organism is slightly different.

The only author who has mentioned these sporozoites is Mingazzini (5), who finds that each spore contains three falciform bodies and a granular nucleus de réliquat. I am at a loss to know how this author has arrived at this result, which I can neither confirm nor express my belief in. I am inclined to think he has inferred the presence of three falciform bodies not from his own observation, but from Schneider's fig. 7 (2, pl. xii). Schneider has drawn in the interior of the spore three oval figures and a patch of granules, which he says nothing about. It seems to me, however, that Schneider did not mean to express hereby the presence of three falciform bodies and a nucleus de réliquat, but rather the presence of a granular undefined mass in the interior. In any case I think we are justified in setting aside Mingazzini's statement, and ascribing eight falciform bodies or sporozoites both to this species and to G. irregularis.

To sum up the above observations, we may give this species the following characters:

Gregarina holothuriæ, Anton Schneider.—Gregarines of somewhat large size, and at first of irregular form, contained in the lumen of the intestinal blood-lacunes (Mingazzini), but later in life becoming regularly egg-shaped, and then enclosed in stalked epithelial vesicles formed by evagination of the walls of the blood-vessels. Body formed of opaque, coarsely granular protoplasm, limited by a distinct cuticle, with two large spherical nuclei, each floating in a clear space free from

granules. The nucleus has a distinct membrane, and contains a granular (?) fluid in which floats a single nucleolus of peculiar vacuolated structure. The cysts are formed free in the body-cavity. The protoplasm segments to form sporoblasts, which develop each into egg-shaped spores, with a funnel-like expansion at the narrow end, and a caudal process formed from the outer layer of the cuticle at the broad end. The spore contains eight nucleated falciform bodies embedded in a granular "nucleus de réliquat," and each provided with a flame-shaped tail.

Habitat.—Intestine, blood-vessels, and cœlom of Holothuria tubulosa at Naples and Nizza.

We shall now proceed to discuss the systematic position of these Gregarines. But first it is necessary to consider one question: are these binucleated adult forms to be looked upon as one individual or two? The only author, as far as I know, who has touched upon this point is Mingazzini (**5**), who considers each specimen to represent a pair of conjugated adults; without, however, excluding the possibility of their double nature being due to fusion of a single individual. He further describes the animals as divided by a septum, on each side of which is one of the nuclei. I have not been able to see a trace of this septum, and much doubt its existence; nevertheless I am inclined to consider Mingazzini's view as the correct one for the following reasons: (1) there are no cases known in which it is the normal condition for a Gregarine to have more than one nucleus; see on this point Bütschli (**6**, p. 523); (2) though it cannot yet be said by any means to be the rule, yet, whenever the life history of a Gregarine has been carefully observed, it is found in the majority of cases that two individuals fuse to form a cyst, whereas here a cyst is formed from a single binucleated adult; and (3) I would call attention to the peculiar Gregarines figured by Sars (**3**, pl. xvi, figs. 2, 3, 5, 6, and 7, *a*, and fig. 8), observed by him in the intestine and blood-vessels of Chiridota lævis, Fabr. sp. (= Ch. pellucida, Vahl sp.). Here one sees little Gregarines attached to the tissues, always in pairs, but quite distinct

from one another. It seems to me not improbable that this represents young specimens of a Gregarine allied to those described in this paper. Nevertheless I do not consider it as by any means proved that these Gregarines are really each a pair of individuals, and have therefore not included this character in the diagnosis of the species.

To discuss the affinities of these forms it will be convenient to begin by tabulating the characters in which the two species agree with, and differ from, one another respectively.

A. They agree with one another—

(1) In the general structure of their cuticle, protoplasm, and nucleus.

(2) In the possession of two nuclei.

(3) In using up all the body protoplasm to form sporoblasts, from each of which a spore develops.

(4) In the shape of the spore, the arrangement of its cuticle, and the possession of a funnel at the narrow end.

(5) In forming eight sporozoites.

(6) In the general structure of the sporozoites, which have a nucleus at the anterior end, to which is attached a flame-like tail posteriorly.

(7) In the fact that both pass the chief period of their existence in the blood-vessels of Holothurians.

B. Leaving out mere details, they differ in the following points :

(1) In form; G. irregularis appears to keep its irregular shape up to the time of encystment, while in G. holothuriæ it is only present in the young stage.

(2) In the presence of a caudal process to the spore in G. holothuriæ, which is entirely wanting in G. irregularis.

(3) Perhaps in the form of the sporozoites, especially in its nucleus.

(4) G. holothuriæ is contained in stalked vesicles formed by evagination of the blood-vessel long before encystment, and breaks loose into the body-cavity to sporulate, while G. irregularis appears not to evaginate the wall of the blood-vessel until ready to encyst, and to sporulate in the vesicle.

Since these differences in two such closely allied forms must be the result of different adaptation to circumstances, we ought to be able to find in the life conditions of these forms some explanation of it, and I believe that such an explanation can be given. As I have shown elsewhere,[1] Holothuria nigra possesses immense numbers of Cuvierian organs which are thrown out on stimulation, and in the ejection the wall of the rectum is ruptured, so that the contents of the body-cavity can escape. If now G. irregularis lived in stalked vesicles while still simply in the adult form, it would often run the risk of having the stalk of the vesicle ruptured, and being thrown out before its time. When once it is encysted, however, it may be of advantage to be thrown out, and thus escape to the exterior. On the other hand, Holothuria tubulosa is entirely without Cuvierian organs, hence G. holothuriæ does not run the same risk of being cast out. In fact, it must be rather hard for the spores in this form to escape, and I am rather inclined to attribute to the caudal process some action in the escape of the spores from the body-cavity, perhaps being used to bore through the tissues in some way. On the other hand, Semper (11) has suggested that the autotomy of Holothurians may be of biological importance to the parasitic Entoconcha mirabilis in their body-cavity, the young of which could become free by producing autotomy through internal stimulation, and the same might apply to the Gregarines. The irregular form is perhaps due to life in the complicated anastomosis of the blood-plexus, and is only retained as long as the animal continues to live in the lumen of the blood-vessel, i. e. throughout life in G. irregularis, but only in the young stage of G. holothuriæ. Thus the difference in form would also be indirectly caused by the presence or absence of Cuvierian organs.

It is obvious that if a genus is to be constructed for these forms, it must not be defined by characters that are not constant in all the species. Armed with this axiom, let us consider previous attempts to classify these organisms.

[1] 'Annals and Magazine of Natural History,' October, 1892.

Cuénot (4) places the three known to him in the genus Syncystis, Aimé Schneider, namely, S. synaptæ from the intestinal vessel and cœlom of Synapta inhærens; S. holothuriæ, Ant. Schn. sp., from Holothuria tubulosa; and S. Mülleri from cœlom of Synapta digitata. He does not appear to be personally acquainted with "Syncystis holothuriæ," or with the fact that it had been described as binucleated by Kölliker and Schneider, or he would certainly not say it was similar to the form he describes, more especially "Syncystis synaptæ" (= Monocystis synaptæ, E. R. L.), in which we may note from his description the following points:—a doubly contoured cuticle; a single nucleus; cyst limited by a cuticle like that of the Gregarine, with in the centre a spherical nucleus de réliquat (a quite unusual use of the term, which is always applied to unused matter in the spore); spores oval or navicular, with three or even four nuclei. In a foot-note we are informed that Professor Aimé Schneider had considered this form as belonging to the genus Urospora. Professor Bütschli also wrote to me "Ein Schwanzanhang der Sporen ist von der Gattung Urospora, Aimé Schneider bekannt, es scheint daher wahrscheinlich, dass die Gregarine der Holothuria zu dieser Gattung gehört." Mingazzini (5), on the other hand, places them in the family Syncystidæ, but establishes a new genus Cystobia for them, considering that they differ from the genus Syncystis, in which the spores have at each pole four diverging bristles (setole), while in the genus Cystobia the spore has only two bristles, and only at one pole. The genus Cystobia is characterised as follows:—"Lives conjugated in special cysts formed in the tissues, especially in the walls of the vasi acquiferi. Cysts proper with the wall covered with little spines. Sporulation complete. Spores very numerous, fusiform, bicaudate, with three falciform bodies." As we have seen, almost the only details in this diagnosis which are correct are "sporulation complete, spores very numerous." In this genus the author puts two forms, Cystobia holothuriæ, Ant. Schn., and a new species, Cystobia

Schneideri, from Holothuria poli and impatiens, which is characterised as follows:—"Has a general facies and a method of sporification similar to that of the preceding species, differs from it in being smaller and much less resistent to the direct action of sea water, while C. holothuriæ can stand it much longer." I should think it probable that no new species of animal which has been described within the last fifty years has been founded on such a meagre and insufficient diagnosis as this—without, moreover, any figures.

Since one of these Gregarines possesses a caudal process to the spore and the other not, it is obvious that this caudal process cannot be used for classification. This at once sweeps away the genus Urospora for these species, and also Mingazzini's arguments for placing them in the family Syncystidæ.

The genus Syncystis was founded by Aimé Schneider (7) in 1885 for a Gregarine found by him in the fat bodies of Nepa cinerea. The body is pear-shaped or spherical, and in the latter forms Schneider was unable to see "la moindre trace d'une division du noyau" (p. 92). Two such individuals fuse before encystment, as occurs in many, if not all Gregarines. The sporulation is not complete, since a central mass of protoplasm remains over. The spores are oval, and usually have four bristles at each end; they contain eight sporozoites, each with a nucleus and nucleolus, "arranged obliquely, giving lines which cross one another from one face of the spore to the other; at the centre a nucleus de réliquat" (p. 94). From figs. 21, 22, and 23, pl. xxiii, it can be seen that the nucleus of the sporozoite is placed in its centre.

If this summary of Schneider's description of Syncystis be compared with that given above of the Holothurian Gregarines there only appears to be one point common to the two—the formation of eight sporozoites in the spore, which occurs also in the Monocystis of the earthworm, and in Clepsidrina ovata, a Polycystid (Schneider, 'Tablettes zoologiques,' i, pp. 25—28, pl. xi), as well as in Coleophora heros (Schneider, op. cit., p. 98, pl. xxv, figs. 11—13, *a*), &c.

so that not much stress can be laid on this point for classification. The spores of Syncystis lack the characteristic funnel of the spores of our Gregarines, and the caudal process of the latter can be in no way homologised (even if it were a constant phenomenon, which is not the case) with the bristles of the spore of Syncystis. Hence I think we are justified in concluding that the Gregarines of Holothurians have no affinity whatever with the family Syncystidæ.

On the other hand, in regard to their double nature, these Gregarines have a considerable resemblance to the remarkable Diplocystis Schneideri described by Kunstler (12) from the body-cavity of Periplaneta americana. This form lives in a conjugated condition, and "presents normally the aspect of two monocystid Gregarines in syzygy, and preparing for encystment," p. 45 (= 21). Each half, however, has a membrana propria, but the whole is surrounded by a general membrane which passes from the one to the other without penetrating their plane of separation. But in the very young stage (pp. 26, 27, pl. ix, fig. 16) it occurs attached to the digestive tract of the Periplaneta in a serous sac, contains two nuclei which differ in structure from one another, and is not divided by a septum. The conjugation takes place very early in the life-history, almost immediately after the intra-cellular phase, p. 61 (= 37), figs. 18, 19. According to M. Kunstler, p. 62 (= 38), the conjugation does not appear to be the result of union of two individuals primitively separate, but a single intra-cellular form divides, to afterwards fuse completely and then to separate again. I am therefore rather inclined, on a priori grounds, to doubt if these observations are quite correct; it seems to me more probable that the little couples shown in Kunstler's fig. 18 are derived from two separate intra-cellular individuals which he has overlooked, as the best of observers might very easily do. In any case I would point out the striking parallel between Kunstler's fig. 16 and my fig. 20.

The spores of Diplocystis are oval or spherical without any appendages. The sporozoites, eight in number, cross one

another obliquely. Hence I do not think the Gregarines of Holothurians can be placed in the genus Diplocystis, though they show a great affinity with it.

Where, then, are these Gregarines to be placed? I suppose if a genus is to be made for them, the genus Cystobia, Mingazzini, has the priority; but the genus remains reduced to the mere shell, the name only, for the kernel, Mingazzini's diagnosis, must be changed, and the genus itself must be removed from the family Syncystidæ. As a matter of fact I do not consider our knowledge of these Gregarines sufficiently advanced as yet to discuss their zoological position within the group Monocystidea. Not until the Gregarines of many Holothurians have been thoroughly worked out and compared can it be known what characters are constant peculiarities and what are merely characters of adaptation. It seems to me highly probable that the different species of Holothurians will prove to have closely allied species of Gregarines, derived from a common ancestor which inhabited the ancestor of the genus Holothuria. In order to obtain characters of classificatory value sufficient to found genera and families, the Gregarines inhabiting allied species of animals should be carefully studied and compared in order to find out in what points they agree and differ. The custom at the present time seems to be, however, to open any animal that comes to hand, and at once describe the Gregarine that inevitably occurs in it as a new genus and species, usually without even giving a figure. Our knowledge of the group is not advanced in the least thereby, but confusion and many vexed questions of nomenclature are stored up for the unfortunate zoologists of the future.

I prefer, therefore, to leave these Gregarines for the present in the old genus Monocystis, and to wait for future researches to determine their true affinities.

As to the development of G. holothuriæ and irregularis from the sporozoite to the adult form, I have unfortunately no observations to offer. As Bütschli says, "we touch here upon the section which is as yet the darkest in the developmental

history of the Gregarinida." It seems most probable that the animals come originally from the intestine, penetrating from thence into the blood vascular system, and that they get into the intestine by the animal swallowing spores with its food.

One cannot but be struck, in considering these forms, by the great resemblance of the adult to an ovum, and of the sporozoite to a spermatozoon. Both these resemblances are doubtless due to the action of similar conditions. The adult Gregarine is a resting cell fed by the surrounding tissues and only biding its time to undergo developmental changes, which it commences, as Wolters (9) has shown, by throwing off half the nucleus as a polar body. On the other hand, the function of the sporozoite is to reach and burrow into a cell, for which purposes an elongate shape and locomotory organs are necessary. It is probable, as Schneider (7, p. 94) has said, that "the spores must be introduced into the digestive tract, and that the sporozoites, set at liberty by the digestive juice, have the energy necessary to perforate the mucosa."

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Addendum.

While the above was in the press a new work appeared by L. Cuénot, entitled "Commensaux et Parasites des Échinodermes (Deuxième Note)," in the 'Revue Biologique du Nord de la France,' vol. v, part 1 (October, 1892). The author describes the Gregarines of Synapta inhærens and digitata, which he now places in the genus Urospora, namely, Urospora synaptæ, Ray Lankester, and U. Mülleri, Giard. The former of these is found under two forms in the adult condition. Cysts are found in the cœlom. The spores have as a maximum four sporozoites; they have at one pole "a tuft [aigrette] of four little bristles," at the other a caudal filament two or three times the length of the spore.

The author does not make any definite statement as to the number of nuclei in the adult, so it may be presumed that there is only a single nucleus. The spores seem to show some resemblance to those of the forms described by me. The tuft of bristles is doubtless homologous with the funnel in the spore of my Monocystis irregularis and holothuria. The presence of a caudal process to the spore is made use of to place these forms in the genus Urospora. After what I have said above on this point further comment here seems to me needless.

On the whole these forms from Synapta have considerable

affinity with my Gregarines from Holothuria, in spite of certain differences, such as the single nucleus and the four sporozoites. It is probable that not much stress can be laid on these points of difference. The double nucleus in Gregarines from Holothuria is probably due, as has been pointed out above, to precocious conjugation, while the number of sporozoites is, of course, dependent on the number of times the nucleus of the sporoblast divides, and is a character which may be subject to variation.

The author also figures and describes the adult and the spores of Lithocystis Schneideri, Giard, from the cœlom of Echinocardium cordatum, which certainly has a striking resemblance to the Gregarines of Holothuria, both in the form of the spores and sporozoites (eight in number), and in the characters of the adult. In the latter M. Cuénot figures a nucleus with vacuolated nucleolus, resembling closely that of the forms described by me. At the narrow end of the spore the author figures a truncated process, which is evidently homologous with the funnel in my two species. Is it possible that this process represents a stage in the development of such a funnel?

It would appear from these facts that the Gregarines of different Holothurians, Synaptids, and Echinoids have a strong family likeness, and that a careful study and comparison of them would furnish valuable data towards a natural classification of this class of Protozoa.

M. Cuénot quotes frequently from a paper by Léger ("Recherches sur les Grégarines") in 'Tabl. Zool.,' vol. iii, 1892. I have unfortunately not been able to see this paper. I gather, however, from M. Cuénot that the author "attributes solely to the form of the spores a value" for classificatory purposes, and "adjourns the generic denomination of every species of which the complete cycle is not known." I think I have sufficiently expressed my opinion above on the value of the form of the spore for classification, and may refrain from further criticism here.

EXPLANATION OF PLATES XXVII & XXVIII,

Illustrating Mr. E. A. Minchin's "Observations on the Gregarines of Holothurians."

PLATE XXVII.

All the figures on this Plate refer to Gregarina irregularis, n. sp., inhabitiug Holothuria nigra.

Fig. 1.—A specimen from the blood-vessels, drawn living.

Fig. 2.—Another specimen from the blood-vessels. Flemming's fluid, borax carmine. Zeiss, compens. ocular 4, obj. B, camera lucida. × 128.

Fig. 3.—Section (from a series of 40 sections, the 15th of the series) through a blood-vessel with the contained Gregarine. Kleinenberg's picric, hæmatoxylin. Zeiss, compens. ocular 4, obj. B, cam. luc. × 128.

Fig. 4.—The inner part of Fig. 3, × 315. Zeiss, compens. ocular 4, obj. D, cam. luc.

Fig. 5.—Another section (34th of the series) passing through the other nucleus of the same Gregarine. Zeiss, compens. ocular 4, obj. D, cam. luc. × 315.

Fig. 6.—The section (33rd of the scries) immediately before that drawn in Fig. 5. Ocular and objective as in the last figure; cam. luc. × 315.

Fig. 7.—The section next but one before the last (31st of the series). Ocular and objective as in the last figure; cam. luc. × 315.

Fig. 8.—Section through another blood-vessel and the contained Gregarine (from a series of 96 sections, 85th of the series). Zeiss, compens. ocular 4, obj. D, cam. luc. × 315.

Fig. 8*a*.—The nucleus from the same section. Compens. ocular 4, obj. F, cam. luc. × 730.

Fig. 9.—One of the stalked vesicles, containing a cyst, from the blood-vessels, as seen living. Drawn with Zeiss, oc. 2, obj. B.

Fig. 9*a*.—The edge of the same in optical section. Oc. 2, obj. D.

Fig. 10.—A portion of the blood-plexus, with a cyst attached.

Fig. 11.—The contents of a cyst teased up. *a*. Drawn living. *b*,*f*. Fixed with picric-osmic-acetic mixture, and stained with Kleinenberg's hæmatoxylin. Zeiss, compens. ocular 4, obj. F, cam. luc. × 730. *a*, *b*, and *c*. Sporoblasts, each with a single central nucleus. *d*,*f*. Nucleated masses of proto-

plasm from the interior of the cyst. *e*. An isolated nucleus from the internal masses of protoplasm.

Fig. 12.—Spores with four nuclei from another cyst, drawn living, using Zeiss, oc. 2, obj. D.

Fig. 13.—Spores from another cyst. *a*. A spore with four nuclei, and *b*, an undeveloped sporoblast, drawn living, using Zeiss, oc. 2, obj. D. *c—h*. Picric-osmic-acetic, Kleinenberg's hæmatoxylin. Zeiss, compens. ocular 4, obj. F, cam. luc. × 730. *c—g*. Spores with four nuclei. *h*. An abnormal sporoblast with five nuclei.

Fig. 14.—Two spores from another cyst after treatment with 10 per cent. sodium carbonate (glycerine preparation). Zeiss, compens ocular 4, obj. F, cam. luc. × 730.

Fig. 15.—From a series of sections through a cyst. *a*. The cyst-wall, covered by epithelium. *b*. A spore with eight sporozoites. Zeiss, compens. ocular 4, cam. luc., obj. F. × 730. *c*. Another spore with eight sporozoites. Zeiss, compens. ocular 4, homogen. immers. 2 mm., cam. luc. × 900. *d, e, f*. Sporozoites from other spores of the same cyst, much enlarged.

Fig. 16.—From a series of sections through another cyst. *a*. Spore in longitudinal section, showing six sporozoites. Zeiss, compens. ocular 4, obj. F, cam. luc. × 730. *b*. Spore in transverse section, showing eight sporozoites. *c*. Another spore in longitudinal section, with five sporozoites. Zeiss, compens. ocular 4, homogen. immers. 2 mm., cam. luc. (with the tube of the microscope drawn out). × 1000. *d, e, f*. Sporozoites from spores of the same section, much enlarged.

Fig. 17.—*a, b, c, d*. Four sporozoites, much enlarged, from the spores of another cyst which was cut into sections.

Fig. 18.—Combined semi-diagrammatic figure of a ripe spore, with eight rozoites. × about 1150.

PLATE XXVIII.

All the figures on this Plate refer to G. holothuriæ, from Holothuria tubulosa, Naples.

Fig. 19.—Some blood-vessels from Holothuria tubulosa, with vesicles containing Gregarines. Drawn living.

Fig. 20.—One of the Gregarines shown in Fig. 19, after fixation with Flemming's fluid and staining with alum carmine. × 210.

Fig. 21.—From a section through a Gregarine, showing the two nuclei (Kleinenberg's picric, borax carmine, hæmatoxylin). Zeiss, compens. ocular 4, obj. D, cam. luc. × 315.

Fig. 22.—*a*, *b*, *c*. Nuclei from other Gregarines in the same series. Zeiss, compens. ocular 4, obj. D, cam. luc. × 315.

Fig. 23.—From a Gregarine fixed with Flemming's fluid, and stained with safranin. Zeiss, compens. ocular 4, obj. D, cam. luc. × 315. *a*. Part of the edge in optical section. *b*. A nucleus.

Fig. 24.—A spore in outline. Zeiss, compens. ocular 4, obj. F, cam. luc. × 730.

Fig. 25.—*a* and *b*. Two spores containing eight sporozoites, from a preparation of Professor O. Bütschli, of Heidelberg. Zeiss, compens. ocular 4, homogen. immers. 2·0 mm., cam. luc. (the tube of the microscope drawn out).

Fig. 1.

Fig. 2.

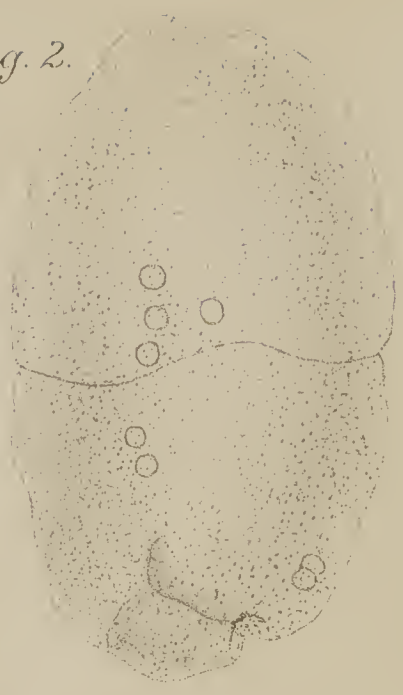


Fig. 3.

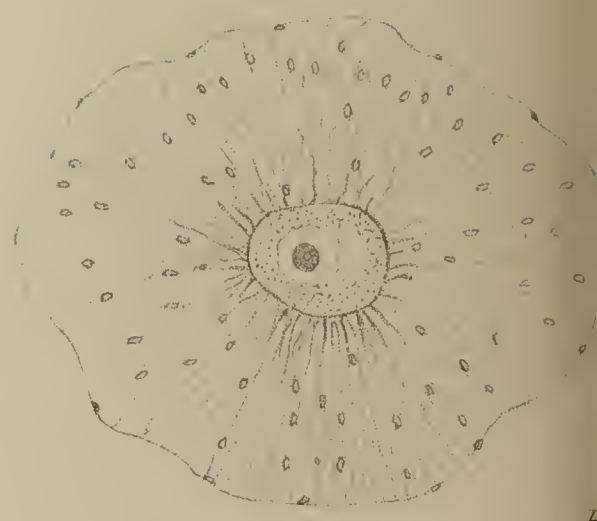


Fig. 7.

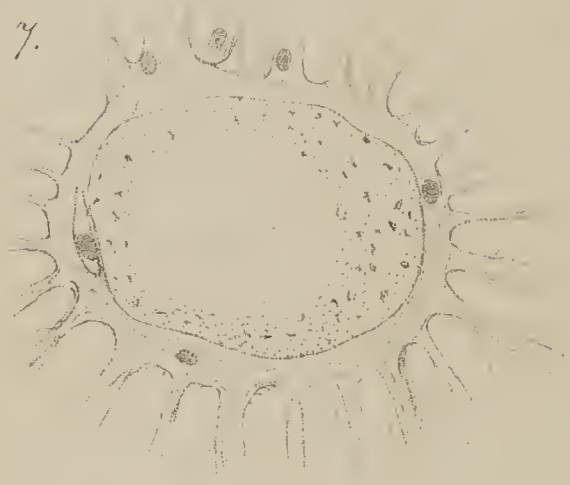
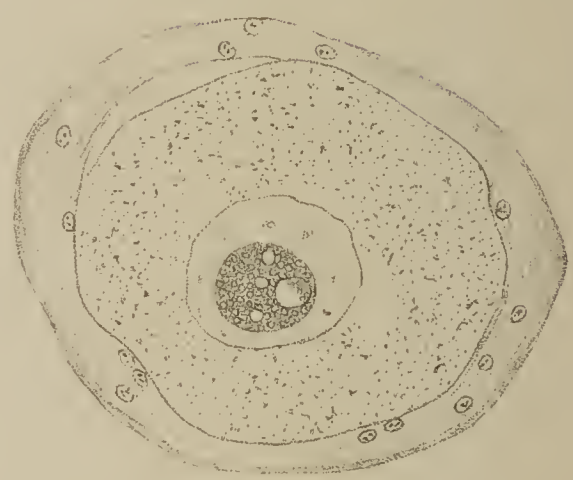


Fig. 8.



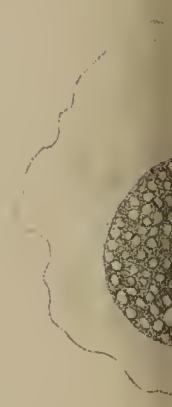
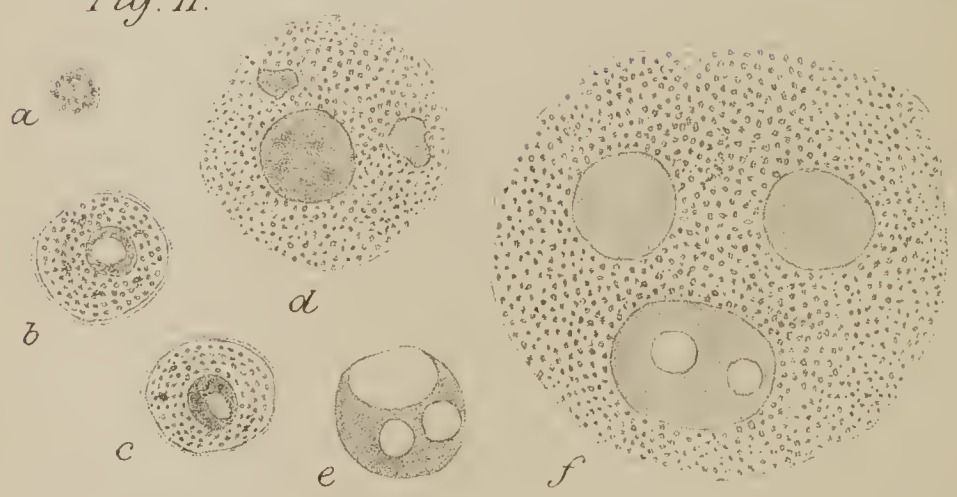


Fig. 11.



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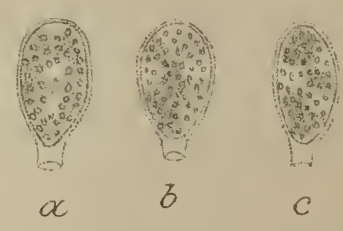


Fig. 13.

Fig. 15

Fig. 16.

Minchin del.

Fig. 5.

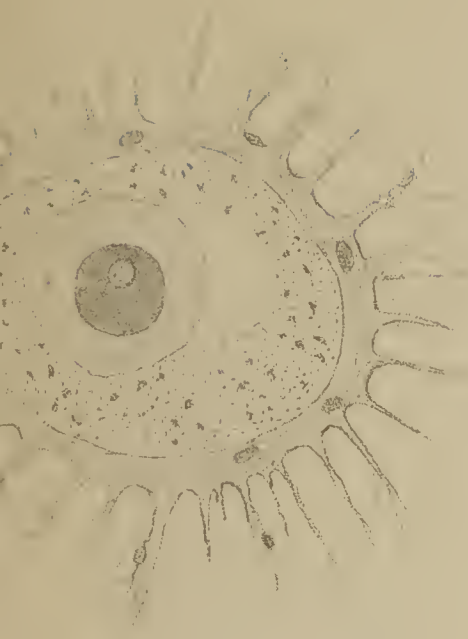


Fig. 6.

Fig. 9.

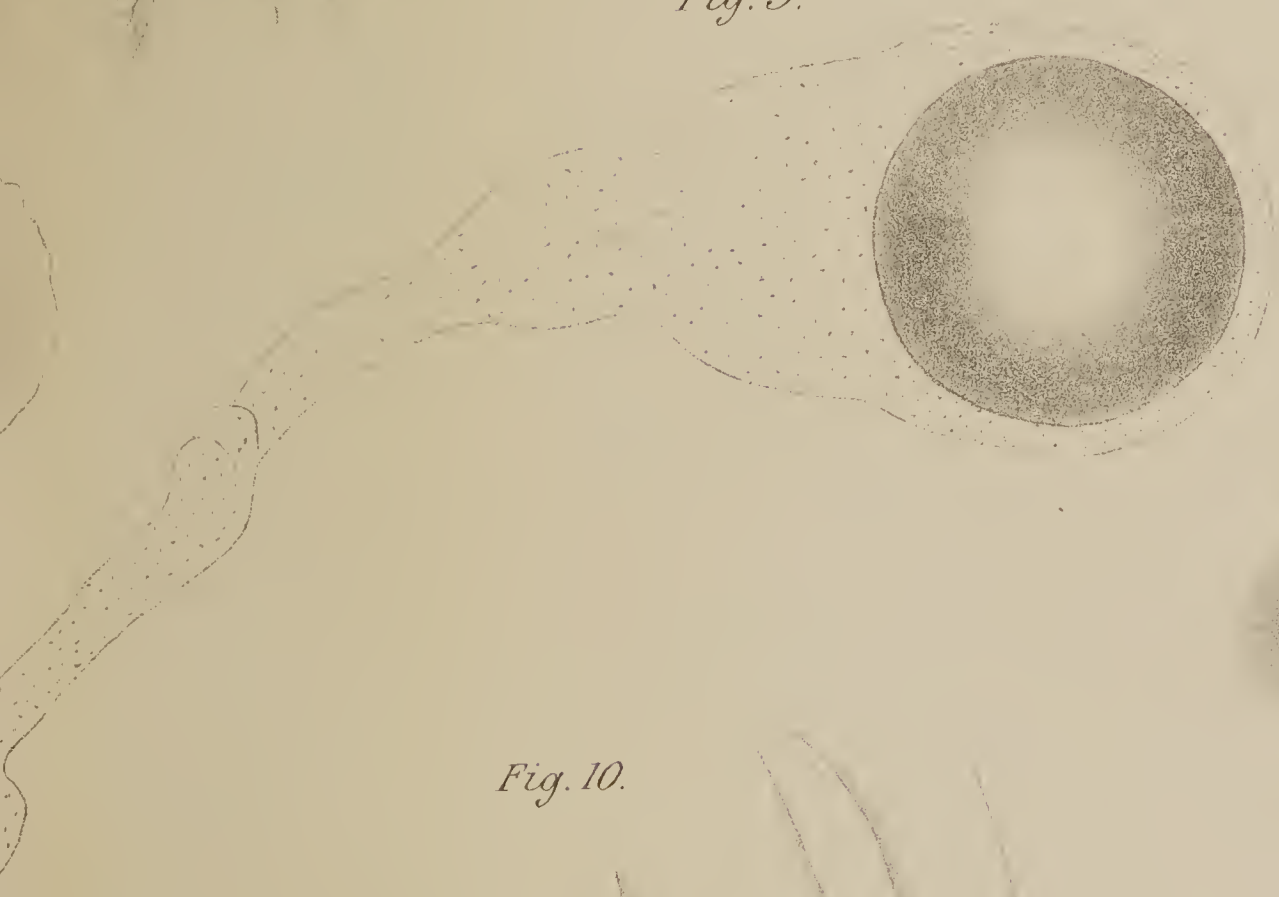


Fig. 9a

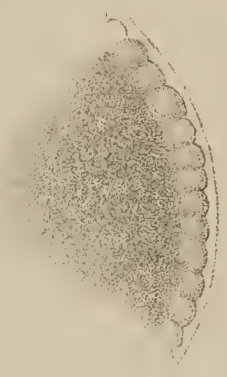


Fig. 10.

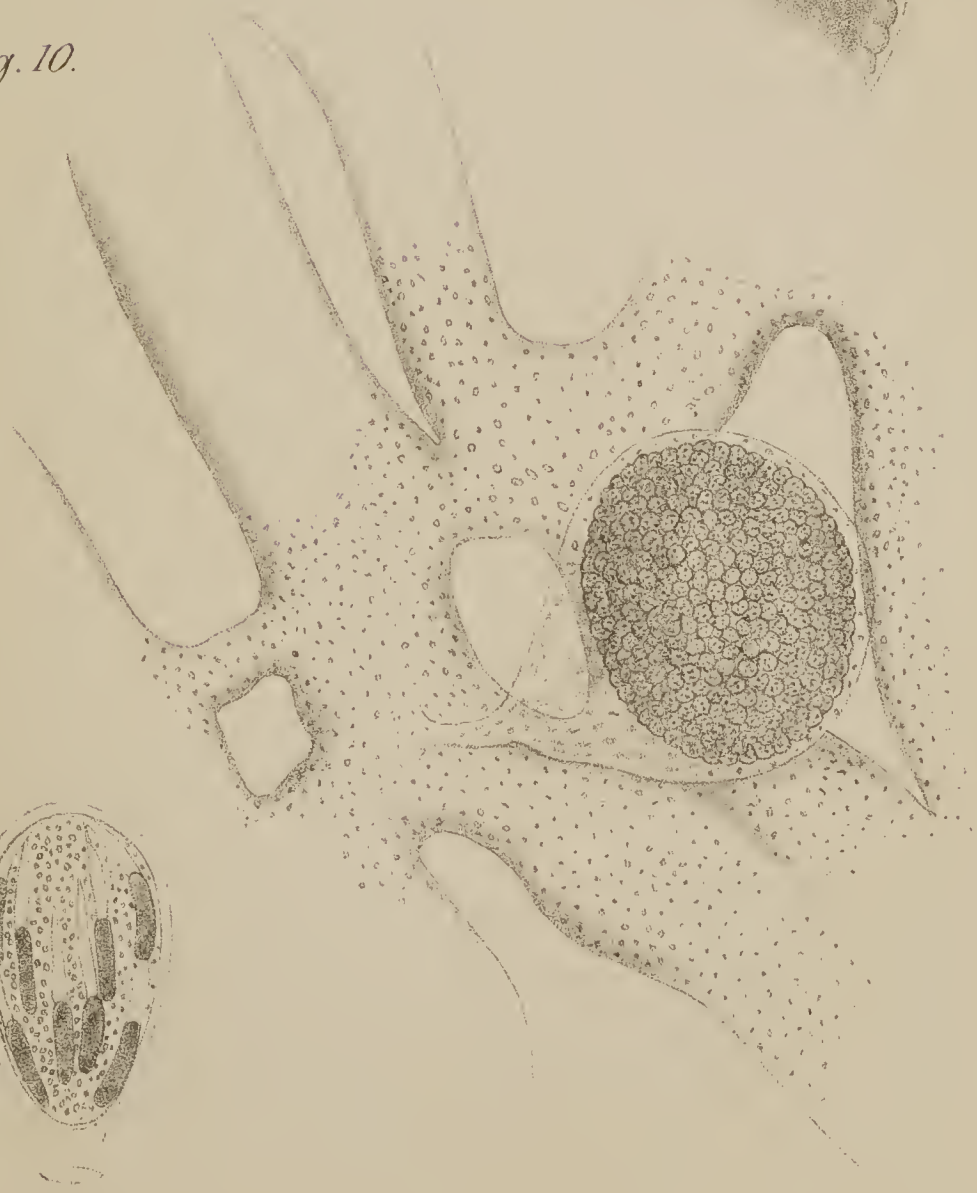
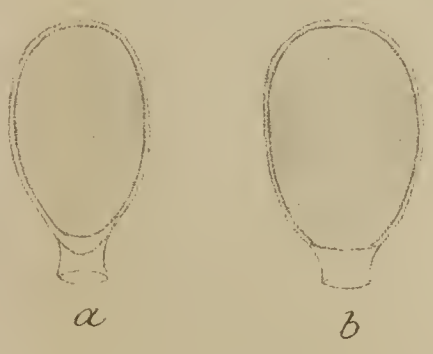


Fig. 14.



a b

Fig. 17.

a b c d

Fig. 18.

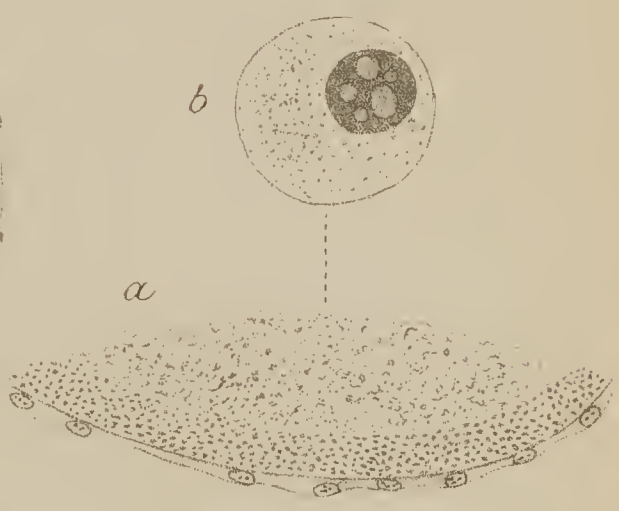
F Huth, Lith^r Edin^r

Fig. 19.

Fig. 22.

Fig. 20.

Fig. 23.



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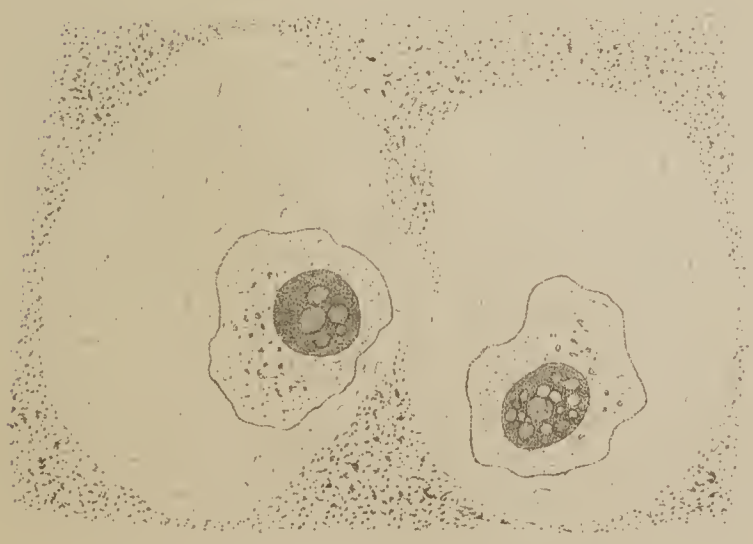
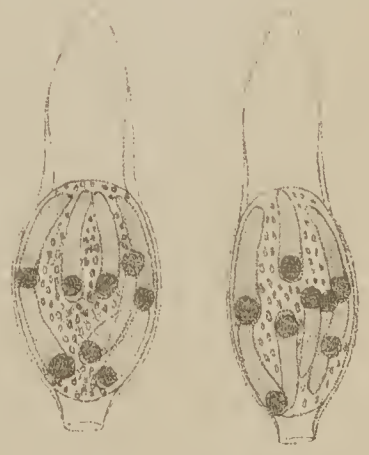


Fig. 24.

Fig. 25.



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F. Huth, Lith^r Edin^r

A New Sporozoon in Amphioxus.

By

E. C. Pollard, B.Sc.

With Plate XXIX.

My work has been carried on in the Laboratory of Comparative Anatomy at Oxford; and I wish at the commencement of this brief notice to offer my best thanks to Professor Ray Lankester, both for allowing me to work here and for his valuable suggestions and help.

Quite recently I had occasion to cut a series of transverse sections through Amphioxus lanceolatus for the purpose of demonstrating the working of the microtome, rather than with any idea of obtaining sections of any particular interest.

To my surprise, however, the series, although cut without any particular care and in a hot atmosphere, proved to be well worth examining, chiefly from the fact that the cochineal stain which was used had differentiated the tissues to a remarkable extent. This differentiation is chiefly noticeable in the intestine, which is stained a deep violet, in strong contrast to the cochineal red of the notochord and other tissues.

On examining the sections a peculiar structure in the intestine at once attracted notice.

In various parts of the posterior region of the gut the epithelium appeared to differ from that of the rest of the wall, the cells seeming to contain much larger nuclei, and being apparently curved round to form small cup-shaped organs (figs. 1—4).

As will be at once seen from the figures, these cups present

on cursory observation an appearance very similar to that of Vertebrate taste-bulbs.

Appearances, however, proved absolutely deceptive, for in thinner sections examined with a higher power the nuclear-like bodies (figs. 1—9, *p.*) were seen to be not nuclei, but each in itself a minute cell parasite, evidently a stage in the life history of a Sporozoon.

Each of these parasites is elongate, tapering at each end, and on an average only ·01 mm. in length.

The protoplasm presents a coarsely granular appearance (figs. 8 and 9), the granules staining more deeply than the rest of the cell protoplasm.

Centrally there is a clearer space, and within this again a deeply staining round body, which I at first took to be the nucleus.

After careful examination of my slides with Zeiss's homogeneous immersion lens I am, however, inclined to regard the deeply stained body (fig. 9, *n.*) as the nucleolus, and the clearer protoplasm (*N.*) in which it is situated as the nucleus.

It is extremely difficult to make certain of this point in such minute organisms, and I have not been able to absolutely satisfy myself as to the presence of a nuclear membrane.

Nevertheless the forms depicted in fig. 9 give one the impression that the part marked *N.* is a large nucleus whose chromatin is all collected into the globular nucleolus (*n.*), and this appearance gains confirmation when compared with the nucleus of other Sporozoa.

Close to the nucleus in many of the specimens a clear round structure may be observed (*v.* in fig. 9, *b* and *c*). This structure is refringent and well defined, but is not visible in every specimen. It has the appearance either of a centrosome or a vacuole. One would not, however, expect to find the former, since there is no sign of nuclear division; whilst if it be a vacuole it is of great interest from the fact that, so far as I am aware, such a structure has never been previously described in a Sporozoon.

The parasites, though occasionally seen at the distal ex-

tremities of the epithelial cells, are usually situated in cavities at the proximal ends of the cells. Sometimes a single parasite is found in an isolated position in the digestive epithelium; but most frequently they occur in groups, and seem to exert some irritating influence over the epithelial cells, causing these to curve round to form the curious cup-like structures drawn in figs. 1 and 4. Not unfrequently the distal extremities of the cells containing parasites are broken away (figs. 7 and 8); but this by no means invariably occurs, and may be due to the preparation of the sections.

The extremity of the parasite nearest the free edge of the cell is in close proximity to the cell nucleus (*M* in figs. 7, 8, and 9). The nucleus of the infected cell, moreover, differs considerably in form from that of the normal epithelial cell (figs. 7 and 8, *M'*). It seems probable that the parasite, by pushing against the nucleus, had altered its form until, as in figs. 7, 8, and 9, *a* and *b*, it has the appearance of a granular cap to the parasite.

I have not seen stages showing the alteration of the nucleus; but Schneider, in his 'Tablettes Zoologiques,' figures such a change brought about by the pressure of a growing Sporozoon (vol. i, pl. ix and xxix). In the form described by Schneider the nucleus is situated at the proximal end of the cell, the parasite being more distal in position, whilst in the form now described the nucleus is nearer the free end of the cell than the parasite.

As for the distribution of these parasites in Amphioxus, they occur all round the intestinal epithelium, but are limited to the posterior region of the gut from the atriopore to the anus. In this post-atrioporal region they may be extremely numerous, the epithelium, as in fig. 3, being crammed with them.

The epithelium of the hepatic cæcum is so similar to that of the intestine that I had every expectation of finding these cells also infected.

Although, however, I have sought with the utmost care, both in my own sections and in some excellent series, for the

use of which I am indebted to Mr. Willey, I have been unable to find any trace of the parasite in the cæcum; and, as a matter of fact, I have never seen it so far anteriorly in the digestive tract.

Further, I regret to be obliged to state that I have not yet succeeded in obtaining any other stage in the life history of this form.

Methods.

From its differentiating properties cochineal is an extremely useful stain for Amphioxus, and the parasites are easily seen in sections prepared with this; but the details of protoplasmic and nuclear structure I have made out best in specimens stained with a mixture of borax-carmine and picro-carmine as prepared by Bolles Lee.[1]

The use of the homogeneous immersion lens was essential, and figs. 6—9 were drawn under this with the aid of a Zeiss's camera.

In conclusion, my sincere thanks are due to Dr. G. H. Fowler, who first drew my attention to an unusual appearance in my sections of Amphioxus, which I investigated with the results now published; to Mr. Willey for the most kind loan of his sections, and to Dr. Benham and Mr. Minchin for ever ready advice and help.

Oxford; October, 1892.

Addendum.

In fig. 10 I have figured specimens of a ciliate parasite which occurs in considerable numbers in the atrium of Amphioxus.

Professor Lankester noticed these years ago, and has recently drawn my attention to them, with the suggestion that the cell parasite described above might possibly be a stage in the life-history of this ciliate form.

[1] Bolles Lee, 'Vade Mecum,' p. 122.

Whether this be so or not, a brief description of this Protozoan may not be without interest, no parasite having been previously described in Amphioxus.

This member of the Ciliata is one of the Aspirotrichous Trichostomata, varying in length from ·4 to ·7 mm. There is a definite mouth and short pharynx in a lateral position (fig. 10, *a*, *O*). A large nucleus is situated more or less posteriorly, and is not unfrequently lobed in a curious fashion (fig. 10, *c*), an appearance which is, however, probably due to shrinkage, since it is not of invariable occurrence.

The cell protoplasm is very granular, the granules sometimes, as in fig. 10, *d*, being extremely large.

These parasites occur in considerable numbers, and are found in the atrium both anterior and posterior to the atriopore.

EXPLANATION OF PLATE XXIX,

Illustrating Miss E. C. Pollard's notice of "A New Sporozoon in Amphioxus."

Reference Letters.

M. Nuclei of epithelial cells, altered in form by pressure of parasites. *M'.* Typical nuclei of normal epithelial cells. *N.* Nuclei of parasites. *n.* Nucleoli. *p.* The parasites. *v.* Vacuole-like appearance.

FIGS. 1—3.—Transverse sections through post-atrioporal region of the intestine of Amphioxus, showing the parasites in groups.

Fig. 1. Zeiss, oc. 2, obj. A.

Fig. 2. Zeiss, oc. 4, obj. B.

Fig. 3. Zeiss, oc. 2, obj. B.

FIG. 4.—Group of the parasites within cells, giving cup-like appearance. Zeiss, comp. oc. 4, obj. D.

FIG. 5.—Small portion of intestinal epithelium, with cells containing parasites. Zeiss, oc. 4, obj. D.

FIG. 6.—Some of the parasites from Fig. 5 under a higher power. Zeiss, comp. oc. 4, homog. imm. lens.

FIGS. 7 and 8.—Groups of parasites in intestinal epithelium.

Fig. 7. Zeiss, oc. 4, homog. imm. lens.

Fig. 8. Zeiss, comp. oc. 4, homog. imm. lens.

FIG. 9.—*d—f*, drawn from parasites found isolated from the cell, probably due to the breakage of the cell by the razor; *a—c*, drawn from groups of parasites seen in Fig. 7. Zeiss, oc. 8, homog. imm. lens.

FIG. 10.—*a—d*. Ciliate parasites occurring in the atrium of Amphioxus. *Nu.* Nucleus. *O.* Mouth. Zeiss, obj. D, oc. 2.

Fig. 1.

Fig. 2.

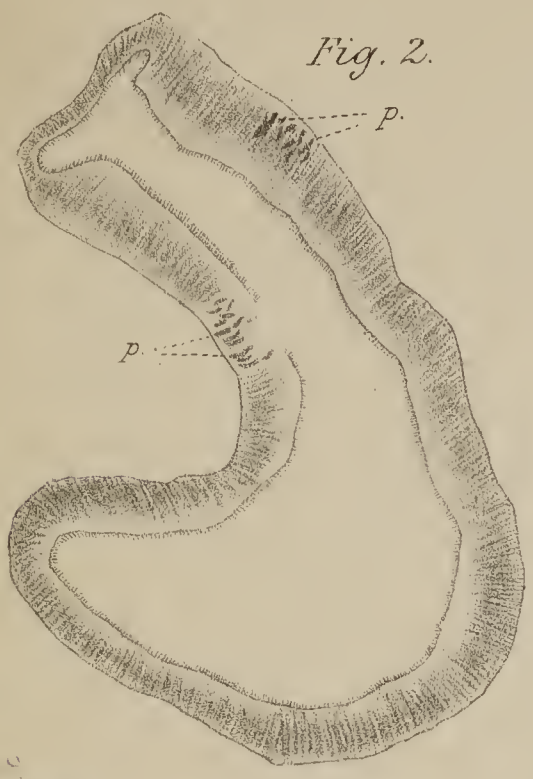


Fig. 3.

Fig. 4.

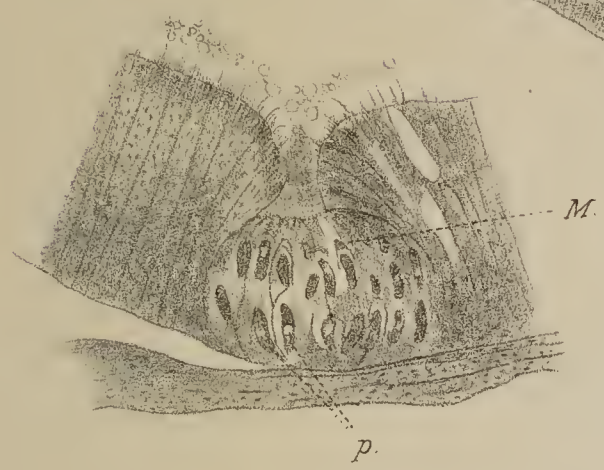


Fig. 5.

Fig. 6.

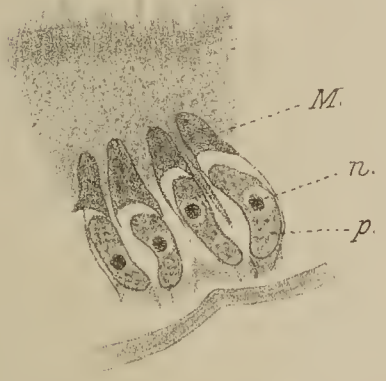


Fig. 7.

Fig. 8.

Fig. 9.

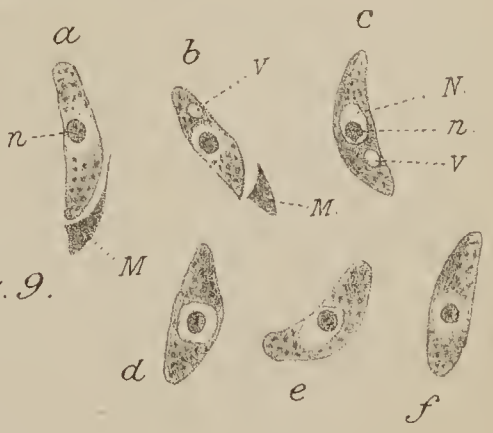
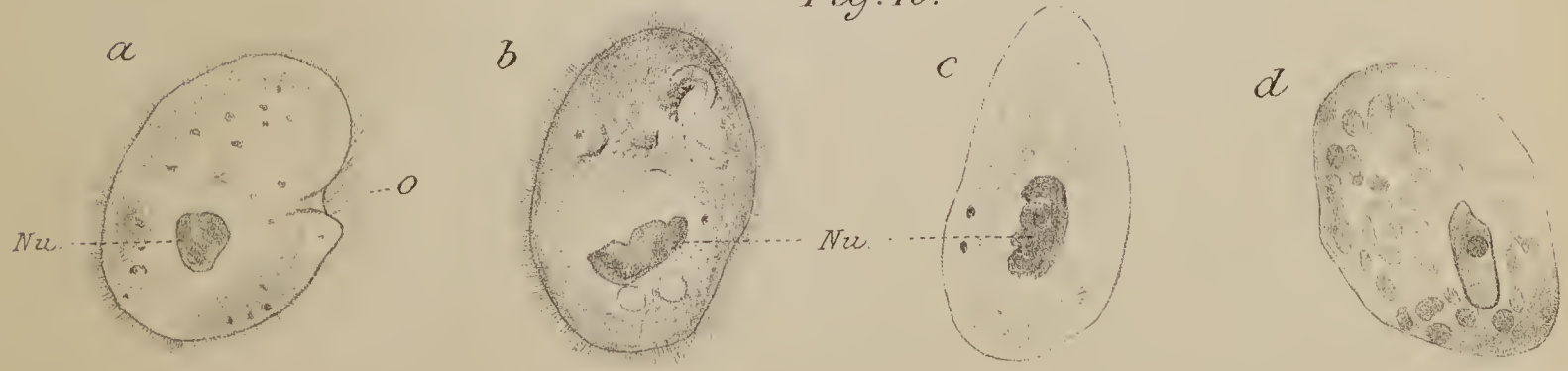


Fig. 10.



E.C. Pollard del.

F. Huth, Lith.r Edin.r

From the Annals and Magazine of Natural History,
Ser. 6. Vol. xi., *April* 1893.

Preliminary Account of the Freshwater Medusa of Lake Tanganyika. By R. T. Günther, B.A.

[Plates XIII. & XIV.]

In August 1891 Mr. F. L. M. Moir, Manager of the African Lakes Company, informed Dr. A. Günther that he had observed Medusæ in large numbers in one of the bays of Lake Tanganyika. "They were about $\frac{3}{4}$ of an inch in diameter, and their rounded top was so clear as to give the idea they were merely circular bodies and not the shape of an ordinary Medusa; the more opaque ovaries gave this appearance." At the same time Mr. Moir kindly undertook to obtain specimens properly prepared with osmic acid; and, thanks to the assistance of Mr. A. J. Swann, these specimens arrived in good condition at the end of last year. This material was placed by my father in my hands for examination and description.

Although Mr. Moir has thus the merit of having been the first to succeed in having specimens brought to Europe, he is not the original discoverer of the species. In fact, from April and during our summer months the Medusæ seem to be exceedingly abundant about the bays of the lake, so much so, that they attract the notice of all visitors.

In December 1883 Professor E. von Martens * communi-

* Sitzgsb. naturf. Fr. Berl. 1883, p. 197.

cated to the 'Gesellschaft naturforschender Freunde zu Berlin' the substance of a letter from Dr. R. Böhm, then travelling in Africa, relating to the discovery of a Craspedote Medusa in Lake Tanganyika. The information to be gathered from Böhm's account was restricted to the following points:—that the Medusa was provided with a velum; that it had a small short broad stomach, at the base of which the genital organs are situated; and, finally, that the tentacles were very numerous and of unequal length. On account of the complete physical isolation of Lake Tanganyika from all other localities from which Medusæ are known, Böhm very justly considered the newly discovered species to be unknown to science, and accordingly proposed the specific name of *tanganjicæ*, leaving the generic name, and at the same time deploring that the absence of all necessary literature prevented him from further determining the zoological position of the species.

Evidently the same animal has since been observed by H. von Wissmann, who, when describing his passage across the lake on the 13th of April, 1887*, says, "I was greatly astonished to observe a number of sea-nettles surround our boat for about half an hour. They were transparent, of the shape of a disk, and like a mark-piece in size; round the edge was a milky circle, hanging down in fibres, by means of which they swam."

Such, then, are the sole facts which, so far as I know, have been hitherto published concerning what is probably the most aberrant of the very few freshwater Medusæ at present known to us.

The specimens were preserved in strong alcohol and were much blackened by the osmic acid which had been employed as a fixing agent, and which had acted especially upon the margin of the umbrella and the manubrium. In size the individuals varied from 1 to 1·8 centimetre across the bell, while the largest specimen was as much as 2·2 centim. in diameter.

The umbrella is characterized by its flattened shape, the diameter being about four times as large as the greatest thickness. The central portion of the umbrella, measuring about two thirds of the whole diameter, is much thickened and has the shape of a nearly hemispherical lens (Pl. XIV. fig. 4), while the peripheral portions are very much thinner. The margin of the umbrella is bent over and incurved towards the mouth. The exumbrella is smooth and covered with an epithe-

* H. von Wissmann, 'Through Equatorial Africa' (English translation), p. 253.

lium of flattened polygonal cells. The velum is well developed in some specimens, but not so conspicuous in others. The circular muscles of the velum (fig. 5, *m.v.*) are arranged on the inner side in separate concentric bands, varying in number according to the breadth of the velum. The muscle-bands near the free margin are always more highly developed than those situated near the attachment of the velum.

The gastrovascular system differs from that of all other Medusæ hitherto described in the relative size of its parts. The mouth and stomach are both circular, widely open to the exterior, and of so great a diameter—two thirds that of the umbrella—that the lips of the mouth probably never completely close the stomach in the adult animal. In all the specimens examined the central portion of the shallow stomach-cavity is almost completely filled with the large central lens-shaped boss of the umbrella (fig. 4), so that the stomach is reduced to a circular trench all round the central boss inside the manubrium, and can hardly be said to possess any central cavity at all. It might be suggested that this extraordinary condition is merely due to post-mortem changes; but the fact that the relative dimensions of the parts do not vary appreciably in any of the specimens examined, seems to me to be sufficient reason for regarding the condition described as the normal one, at any rate when the animal is not feeding. A possible explanation of this curious dilatation of the mouth and stomach was suggested to me by Mr. G. C. Bourne. It is obvious that any increase in the diameter of the mouth and stomach would involve a corresponding increase in the circumference of the manubrium, which, as will appear in the sequel, is the bearer of the reproductive organs. The large size of the mouth would appear, then, to be correlated with an enlargement of the area upon which the reproductive organs, sexual or asexual, are developed.

The slightly thickened margin of the mouth is quite simple, without processes of any kind. The radial canals are four in number in the majority of individuals; but instances of the occurrence of five or six seem to be by no means rare, specimens with six being rather more numerous than those with five. The radial canals radiate from the stomach in a more or less horizontal plane, but assume a more vertical direction just before they enter the ring-canal, in consequence of the inflexion of the margin of the umbrella. The ring-canal varies in size in different individuals; it is lined by an epithelium of small squarish cells, similar to those lining the radial canals. On the outer side of the canal, however, these cells are in very great numbers, forming a lobulated mass

projecting into and partly blocking up the lumen of the canal (fig. 5). Hollow cavities often occur in this lobulated mass of endoderm-cells.

As in *Limnocodium*, the tentacles are very numerous and may amount to over two hundred in number. In some of the smaller specimens the four primary perradial tentacles are conspicuous on account of their greater length and thickness, but in most of the larger examples they are almost equalled in point of size by the interradial and even the adradial tentacles, so that they are no longer readily recognizable. Alternating with these primary, secondary, and tertiary series tentacles of the fourth and even of the fifth and sixth orders arise with great regularity, and it is only when the seventh order of tentacles are intercalated that the typical regularity of arrangement cannot be further traced. In preserved specimens the relative length of the tentacles varies to a great extent, indicating a considerable capability of contraction and extension. The tentacles are hollow, the lumen of the larger tentacles at any rate being clearly continuous with the lumen of the ring-canal. The lumen of the tentacles is lined with large, thin-walled, columnar endoderm-cells, which are continuous with the endodermic lining of the ring-canal (fig. 5). The transition from the tentacular endoderm-cells to those of the ring-canal is very abrupt. The thread-cells are of small size and generally arranged in little wart-like groups or batteries (fig. 5), which are more or less disposed in whorls and which are especially closely set at the tips of the tentacles.

The proximal ends of the tentacles are all adnate to the margin of the umbrella for some considerable distance (figs. 4 and 5, *te.*), the older tentacles being adherent along a greater length than the younger ones. At the points of fusion the tentacles become partly imbedded in the substance of the margin of the umbrella, while the tentacular ectoderm becomes continuous with that of the exumbrella, so that in a section across the line of fusion an ectoderm lamella is seen between the mesoglœa of the tentacle and that of the umbrella (fig. 5, *ect.*).

On the side of the ring-canal opposite to that at which the tentacles arise and just external to the origin of the velum is situated a circle of sense-organs. These vary considerably in number and are arranged at irregular intervals, so that neither their number nor grouping can be brought into relation with that of the tentacles. The structure of these marginal bodies is peculiar.

They are refringent egg-shaped bodies attached to one side of a round or ovate capsule, the walls of which are lined with

a flattened epithelium (fig. 7; *s* in figs. 4 and 5). These egg-shaped bodies are composed of numerous cells and apparently attached by a thin stalk or thread to that side of the capsule which is nearest the ring-canal. The basal cells of the marginal bodies have a granular and opaque appearance, being coloured dark brown by the action of the osmic acid. The apical cells, however, are quite clear and refringent (fig. 8). These extraordinary bodies at once recall the corresponding structures in *Limnocodium* described by Professor Ray Lankester*, to which they bear a remarkably close resemblance. At the same time they differ in structure from all other sense-organs hitherto described in Medusæ, the chief difference between the marginal bodies of *Limnocnida* (as I shall call the Tanganyika Medusa) and those of *Limnocodium* consisting in the absence of any tubular extension of the capsules into the adumbral ectoderm layer of the velum as is the case in *Limnocodium*. Another less important point of difference lies in the marked contrast between the granular basal cells and the refringent apical cells in the marginal bodies of *Limnocnida*. However, in spite of these differences there is a very great similarity of structure in the organs of both, and probably the marginal bodies of *Limnocnida* will be shown to be endodermal in origin, just as the "refringent bulbs" of *Limnocodium* have been proved to be.

Among the individuals of *Limnocnida* examined some were found to have the outer wall of the manubrium quite smooth, while others have the proximal half of the manubrium covered with small swellings visible to the naked eye. When subjected to microscopic examination the individuals with the smooth manubriums turned out to be males and females with the external wall of the manubrium covered with spermatozoa or ova in all stages of development.

The other set of individuals with the small swellings proved to be examples showing stages of bud-formation. Buds may originate anywhere on the basal half of the manubrium, so that in some specimens several rows of buds occur, completely encircling that organ.

As far as the method of bud-formation has been observed at present, it appears that the young buds first arise as outgrowths on the external wall of the manubrium. Besides these, a certain number of older buds with rudimentary tentacles occur, projecting into the stomach and presenting the appearance of having actually grown through the

* "On *Limnocodium Sowerbii*, E. Ray Lankester," Quart. Journ. Micr. Sci. vol. xx., 1880.

wall of the manubrium. I hope, however, to be able to supply further details of this interesting process of bud-formation in a subsequent paper.

As the Tanganyika Medusa is still without a generic name, I propose that of *Limnocnida* for it, with the following characters :—

Limnocnida, gen. nov.

Umbrella flat, almost disk-like, about four times as broad as high, with a lens-shaped thickening in the middle. Tentacles very numerous, hollow, with bases partly imbedded in and adnate to the umbrella margin. Marginal sense-organs situate along line of attachment of velum, composed of a multicellular mass of refringent cells enclosed in a roundish capsule. Mouth round, two thirds the diameter of animal. Manubrium very short. Stomach shallow, of same diameter as mouth. Radial canals four. Reproduction by budding. Sexual organs situated on the manubrium.

Limnocnida tanganjicæ (Böhm).

Size : diameter of umbrella $\frac{7}{8}$ inch.
Loc. Lake Tanganyika.

As my knowledge of the significance of several points observed in the general anatomy of this freshwater Medusa is as yet very imperfect, I must reserve a more detailed account of these, as well as all discussion of the probable affinities and systematic position of *Limnocnida*, for another paper. If a place has to be found for *Limnocnida* in Hæckel's System of Medusæ we are beset with almost the same difficulties as those which presented themselves in the case of *Limnocodium*. The same battle will have to be fought over again, only the field is changed. Those who considered *Limnocodium* to be one of the Leptomedusæ will refer *Limnocnida* to the Anthomedusæ, while those who regarded *Limnocodium* as one of the Trachomedusæ will have to place *Limnocnida* among the Narcomedusæ.

EXPLANATION OF THE PLATES.

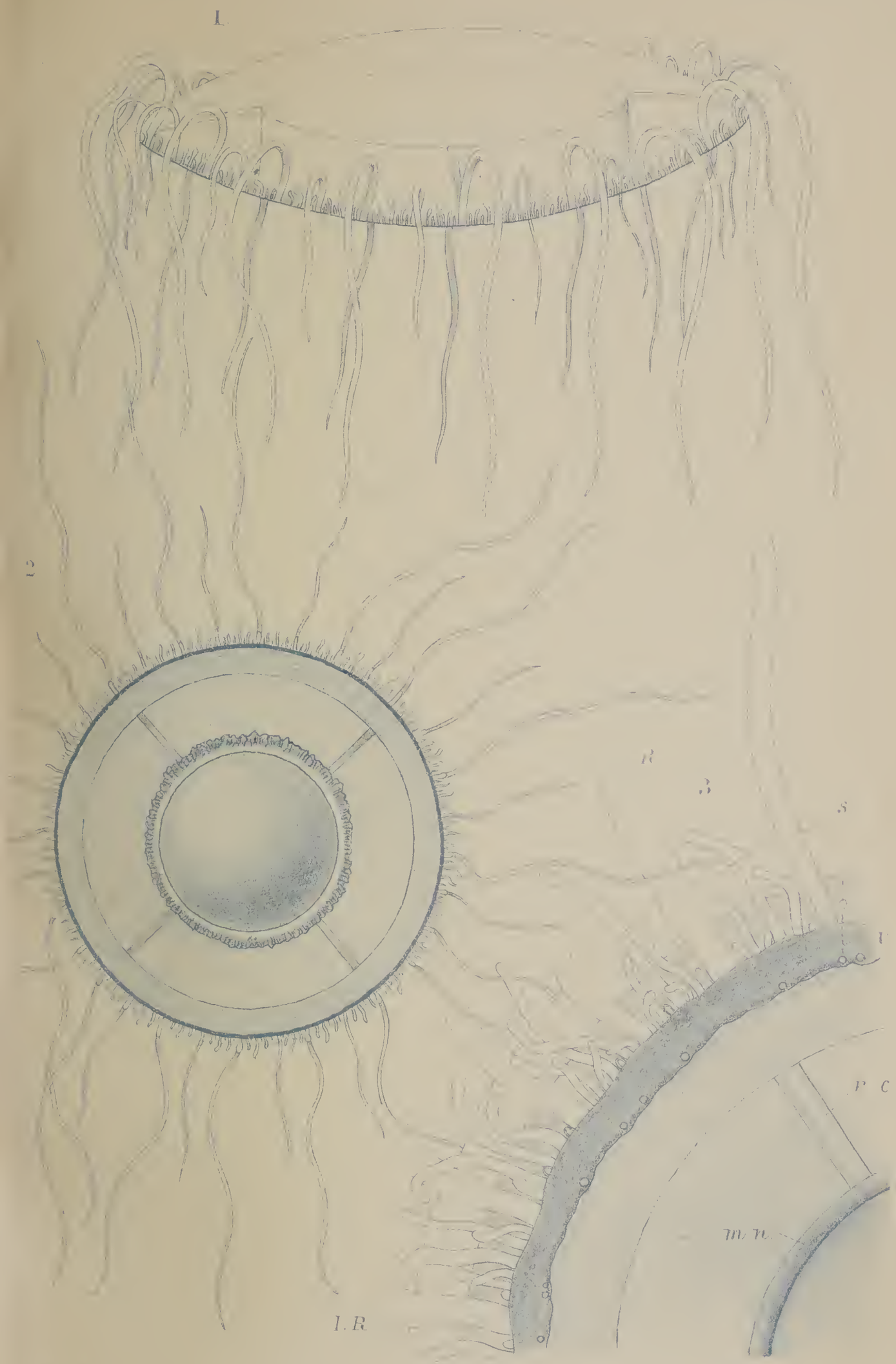
Plate XIII.

Fig. 1. Side view of *Limnocnida tanganjicæ*, × 4.
Fig. 2. Ventral view of ditto, × 3.
Fig. 3. Ventral view of a portion of the periphery of the disk, × 9.

Plate XIV.

Fig. 4. Diagram of a transverse section passing along a radial canal on the right hand side but not on the left.
Fig. 5. A radial section cut a little to one side of the opening of a radial canal into the ring-canal, × 60.
Fig. 6. A portion of a tentacle, showing the arrangement of thread-cells.
Fig. 7. A tangential section through two adjacent marginal sense-organs.
Fig. 8. A marginal body seen in longitudinal optical section.

c.c. Circular canal.
ect. Ectoderm.
e.l. Endoderm lamella.
end. Endoderm.
gem. Medusa buds.
IR. Interradial tentacle.
mn. Manubrium.
ms. Mesoglœa.
m.v. Muscles of velum.
R. Radial tentacle.
r.c. Radial canal.
s. Marginal sense-organ.
te. Tentacle.
v. Velum.



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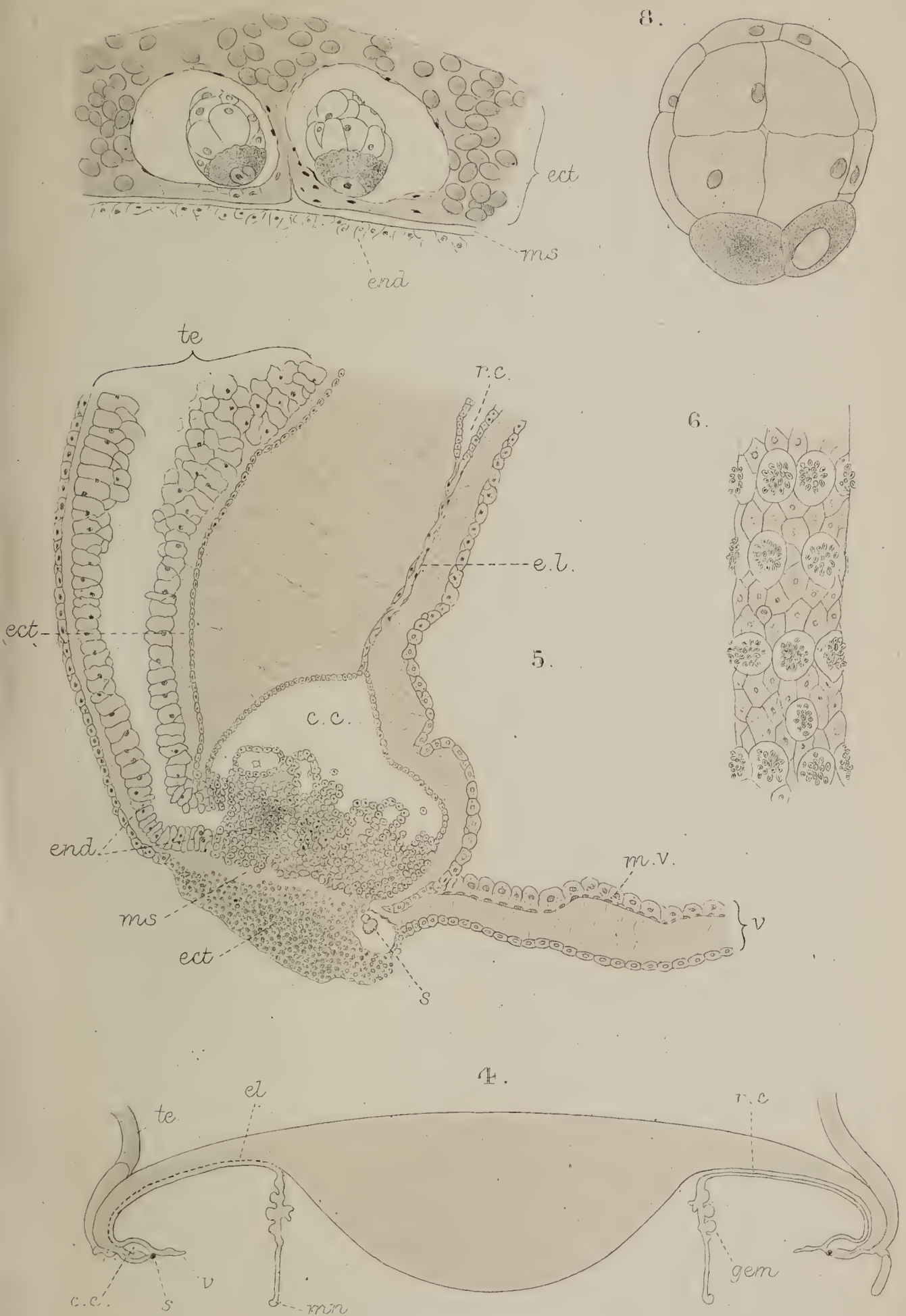
LIMNOCNIDA TANGANJICÆ



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LIMNOCNIDA TANGANJICÆ.

Description of a New Species of Moniligaster from India.

By

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With Plate XXXII.

In June of the present year, 1892, my friend Professor Bell sent me a specimen of a worm collected on the Nilgiris by Mr. T. R. Henderson, which forms a new species of the genus Moniligaster, Perrier, and for which I propose the name M. indicus.

At first I imagined that it would be one of Dr. Bourne's species, but it agrees with none of them in the few—the very few—characters given by him; he practically only gives the position of the gizzard in his seven species, and even this in such a way as is scarcely sufficient for identification; for he does not state how many constrictions are present, i.e. whether there is a separate portion of gizzard to each somite passed through. We await impatiently a more detailed description of the several interesting species, especially of M. sapphirinaoides, which has been so long promised to us.

The position of the various genital pores in Moniligaster by the repeated contributions of Mr. Beddard (1, 2, 3, 4, 5), as well as by those of Rosa, Bourne, and Michaelsen, has now become definitely ascertained; and I much regret that my figure representing the genital organs of this genus, published in my "Attempt to classify Earthworms," on p. 295, is

wrong, owing to my having followed Dr. Horst's account of M. Houtenii, which appears to have the organs posterior to their position in the other species.

This octochætous, meganephric genus is distinguished, as has been pointed out by recent writers, by the following external characters:

(*a*) The male pores (a single pair) between Somites x and xi.

(*b*) A single pair of spermathecal pores between Somites vii/viii.

(*c*) A pair of oviducal pores between Somites xi and xii.

(*d*) Nephridiopores in line with the dorsal (or outer) couple of chætæ.

Internally the following features may be taken as characteristic:

(*e*) The gizzard constricted by one to four narrow, fibrous, annular bands at the septa, giving the "moniliform" appearance indicated by the generic name.

(*f*) Absence of calciferous or other enteric diverticula.

(*g*) A single pair of spermathecæ in Somite viii, with very long, narrow ducts.[1]

(*h*) A single pair of sperm-sacs, supported by the septum between Somites ix and x, but belonging to the former; the sacs are independent, and each encloses the testis and the spermiducal funnel.

(*i*) A single pair of atria (prostates), of varied size and shape.

(*j*) A large ovisac, which may extend through several somites.

M. indicus, n. sp., which forms the subject of the present paper, may be diagnosed as follows:

(*a*) Length 5½ inches (13·75 centimetres).

(*b*) Body consists of about 150 somites.

(*c*) Ventral intersetal space is rather wider than the lateral space (or, as a formula, I—I > II—III).

[1] The apparent exception in M. japonicus, Mich., requires further investigation.

(*d*) The septa VI/VII, VII/VIII, VIII/IX are thick, but not so thick as in other species.

(*e*) Gizzard occupies Somites XIII, XIV, XV, XVI, with annular bands separating the four muscular regions.

(*f*) Atrium (prostate) large, spherical, lying in Somite XI.

(*g*) Spermatheca nearly spherical; the duct opens to the exterior through a muscular sac, subdivided into an anterior and a posterior lobe by the septum VII/VIII.

Description of M. indicus, n. sp.

I. External Anatomy.

The size of the present species has just been stated, and it appears to be of some importance, as there is a great range amongst the species; for example, M. japonicus and M. Barwelli is only 28 mm., M. Deshayesi 150 mm., whilst M. Houtenii attains the length of one and a half metres. Of Bourne's seven species, only M. ruber is definitely measured, its length being 100 mm.

As in all other species, with the exception of M. sapphirinaoides, no clitellum was present; the worm was evidently not quite sexually mature, as deduced from the condition of the genital organs. As Beddard (5) and myself (6) have previously suggested, the clitellum may be a more transient structure than in other macrodrilous Oligochæta; and it would be very interesting, and even important for systematic purposes, to know the minute structure of the clitellum in Bourne's species. Does it agree more closely with the microdrilous clitellum, or is it several cells thick, as in Lumbricus, &c.?

The colour of the worm during life is unknown to me. In the spirit specimens the dorsal surface is very much darker—a greeny brown—than the ventral and lateral surfaces; there is a very sharply marked line of separation between the two colourings, and not a gradual paling out as in many other worms.

The worm is rather flattened, and the posterior end, which is lighter in colour, tapers off to a point, apparently in the same sort of way as in M. robustus, A. G. B., for which species I at first took it; but in that species the gizzard differs in extent and position.

The prostomium is rounded, not embedded in the peristomium at all, but is retracted in the same sort of way as Beddard (5) found in his species.

The somites are separated by deep intersegmental grooves; the first and second, as Beddard points out in his last contribution (5) to the anatomy of M. Barwelli, are very short, the two together barely reaching the length of the third somite.

The chætæ are of the normal shape (fig. 2), and do not agree with those figured by Horst for M. Houtenii, nor with those figured by Beddard (5); they are small, as in the other species, measuring 2 mm.; the free end is rather more hooked than in M. Barwelli. All four couples of chætæ in the present species are on the ventral surface, so that none are visible from above. Their arrangement, as I have inferred above, is of some specific importance. In all species of Moniligaster the individuals of each couple are very close together, and the space between the two ventral couples—i. e. the ventral space—may be equal to, greater than, or less than the lateral space or distance between the dorsal and ventral couples of either side (see fig. 1).

Thus in M. japonicus, Mich., M. Beddardii, Rosa, the ventral space (V) = the lateral space (L); in M. Barwelli, M. uniquus, A. G. B., $V < L$; in M. grandis, A. G. B., as in the present species, $V > L$; whilst in M. Houtenii $V = 2L$.

In the remainder of Bourne's species no reference is made to this point.

The nephridiopores appear to commence in Somite VI, but on dissection I find nephridia anterior to this.

I failed to discover any dorsal pores, either by means of a lens or by mounting a piece of the body-wall in Canada

balsam; but in other species they are apparent, viz. in M. Barwelli and M. Beddardii.

The genital pores have the position normal for the genus, and I found it quite easy to recognise all three pairs (fig. 1); with regard to the male pores, however, I was at first deceived by an apparent slit in the hinder part of Somite x; this turned out to be merely a groove (fig. 1, *x*), due, no doubt, to the shrinkage of the large mass of muscle attached here around the atrium. The groove is bounded anteriorly by a fairly prominent ridge, and presented the appearance figured by Beddard (5, fig. 1), and indicated by him as the male pore itself. I find, however, that the true pore does not correspond with the position assigned to it by him for M. Barwelli; and in this point I am in agreement with Michaelsen's description of M. japonicus (9), where the pore is at the apex of a small tubercle, in front of which is a transverse groove. It is probably a matter of preservation whether the tubercle is prominent or not. My own specimen was very soft and ill-preserved.

The position of the atriopore (fig. 1, ♂) between the dorsal and ventral couples of chætæ agrees with that ascribed to it by previous writers.

The oviducal pores are small but distinct slits in the groove between Somites XI and XII, in line with the ventral couple of chætæ.

The spermathecal pores are larger, and, as in other species, are in line with the dorsal couple of chætæ; in M. Deshayesi, however, the pore is stated to be in line with the "inferior chætæ."

II. Internal Anatomy.

It is to the generative organs that the lumbricologist first turns his attention in opening, or otherwise examining, a worm, and naturally these organs are more engaging, so to speak, in a genus about which such diversity of statement exists, or has till quite recently existed, as to the position of

the various constituents. I have already referred to the uncertainty as to the precise somites to which the different organs belong, which has resulted from the descriptions of Perrier, Beddard, and Horst. But now that a greater number of species are known, some of them of fairly large size, we find Perrier's original statements are correct with regard to the position of most of the genital organs, and that Horst's numbers alone differ by being greater by a single unit. Beddard's original description has been modified by his discovery that his apparent first somite really consists of Somites I and II. The positions attributed to the organs in the species examined by Rosa and Michaelsen, and in the present one, all agree with Beddard's amended and Perrier's original numbers. But nevertheless there still remain certain points on which some discrepancy or uncertainty exists, both with regard to exact position and minute structure. Some of these I hope to clear up, or at any rate to advance, though, owing to the poor condition of the worm, my contribution to the histology of Moniligaster—of which we know very little indeed—is very imperfect.

The single pair of sperm-sacs (figs. 3—5) occupies partly Somite IX and partly X. On the animal's left side the sac appeared to be strung up by the Septum IX/X attached round its equator. In reality the septum is pouched, and the sperm-sac, as figs. 3 and 4 will show, projects into Somite IX through the wide aperture of this pouch.

On the right side, however, the pouch was deeper, so that at first sight the sac appeared to lie entirely in Somite X; but I could trace the Septum IX/X behind the sac, and sections show me that the sperm-sac belongs, as Beddard has already suggested, to Somite IX.

Each sperm-sac is nearly spherical, and is not so simple as in M. Barwelli, for I find that the cavity is not undivided, as Beddard figures and states, but is traversed by bundles of muscular fibres in different directions (fig. 5, *trab.*), between which lie the groups of developing spermatozoa. The trabecular structure is certainly not so highly developed as

in Perichæta, Lumbricus, and other genera, but it is as certainly not entirely absent.

Beddard has laid great stress on the simplicity of the sperm-sac in associating Moniligaster with the Microdrili or "Limicoline section" of the Oligochæta. Here, then, we have still another apparent distinctive character between "aquatic" and "terrestrial" Oligochæta breaking down, and that within the limits of one and the same genus; and it is gradually becoming more and more impossible to characterise differentially the two groups, for in fact they verge into one another at almost every point.

The two sperm-sacs are entirely independent of one another. Each contains a testis and spermiducal funnel.

The testis (fig. 5) is digitate and attached to the hinder wall of the sac, i. e. to the Septum IX/X. The funnel—we cannot call it a "rosette"—of the sperm-duct is a simple, wide, ciliated tract of the hinder wall of the sac (fig. 5). The cells are tall, and thus readily distinguishable from the flattened cells which elsewhere form the wall around it.

This flat funnel can be seen through the thin wall on dissection, and the sperm-ducts can be seen passing away from it (fig. 4).

As to the point of attachment of the testis, I find that it is independent of the funnel. Rosa figures it, both for Moniligaster Beddardii and for Desmogaster, attached to the funnel near to its centre. Beddard also in one figure (fig. 8) represents the testis arising from the funnel, whilst in fig. 9 he shows it at its side. In my own sections the testis lies nearer the middle line of the body than the funnel, so that the two structures are not at their best in any one given section. Perhaps Rosa's diagram is in this point merely diagrammatic.

The sperm-duct is very delicate and very greatly convoluted (fig. 4), much more so than is indicated by either Beddard's or Rosa's figures; it more nearly approaches the condition represented by Perrier (pl. iv, figs. 81, 83), though this zoologist appears to have been disinclined to regard the

"feuillets blancs" as forming part of the sperm-duct, for it would, says he, give such an enormous length to it.

I may mention that in Perrier's species the sperm-duct, which is represented as a comparatively thin coiled duct, appears to pass through a mass of isolated white leaf-like structures set round the duct as an axis. A microscopical examination of these "feuillets" showed that they consist of a very fine coiled duct surrounded by a thin membrane (his fig. 83), and I think there can be no doubt, from the condition present in M. indicus, that this duct in the "feuillet" is part of the sperm-duct itself, and not an appendix thereto. In other species, so far as descriptions go, the duct is not of so great a length. The cells lining the duct are striated as in other worms (fig. 12), but I have never been able to detect hitherto the boundaries of the cells; here, however, they are very plain, and the cells large. In many earthworms the nuclei are flattened, but here, as in aquatic forms also, they are spherical.

In M. indicus the greater part—nearly the entire length—of this fine, convoluted sperm-duct lies in Somite IX below the sperm-sac (figs. 4, 5). It passes through the septum near the body-wall, which it enters, traverses the short distance between this septum and the prostate, embedded in the longitudinal muscle, and enters the atrial wall (prostate) at its anterior end (fig. 5); passes along the dorsal wall of the prostate, perforates the glandular coat, and opens into the atrial cavity at the apex of a slight prominence in the wall (figs. 5, 8). This condition of the duct is very similar to that described by Rosa for Desmogaster doriæ, and so far as the præseptal portion is concerned agrees with Michaelsen's description of M. japonicus.

The prostate is a hemispherical structure occupying the greater part of the length of Somite XI, at the anterior margin of which it opens to the exterior; it also encroaches to a slight extent on to Somite X, to which it probably belongs morphologically.

It is about half (linear) the size of the sperm-sac, larger

than the ovoid prostate of M. Barwelli and M. Beddardii, and unlike these is bound down to the body-wall by special muscles; if it were placed on end with its morphologically dorsal (its actual posterior) end upwards it would resemble the condition in Beddard's species. The hemispherical glandular part is seen in sections to be provided with a duct dorso-laterally compressed and underlying the glandular part. In the other species, so far as is described, the prostate is elongated, and is very large and extensive in M. Deshayesi.

We have no information as to its shape, which is apparently a good specific character, in any of Bourne's species.

There is a very peculiar arrangement of muscles in connection with the atrium which has not hitherto been recorded in any earthworm.

A sheet of muscles, or rather a series of flattened bundles of muscle-fibres, passes obliquely across the body-cavity from their origin in the body-wall above the lateral line to their insertion in the wall of the prostate. On dissection, when the sides of the body are pinned down, this sheet is of course horizontal; in the natural position, however, it is an oblique, transverse sheet, such as exists almost universally in the Polychæta, where, however, it is generally in relation with the chætophores at its outer end.

In Somite x, immediately in front of the atrium, a similar sheet of muscles exists, reaching nearly to the level of the inner chætæ ventrally, and having the same origin as that in Somite xi. In Somites vii, viii, ix quite a similar arrangement obtains, though, as we get forwards, the muscle bundles are smaller and smaller.

These recall the "arciform muscles" recently described by Cerfontaine[1] in Lumbricus, but which pass, not from the lateral to the ventral surfaces, but from one side to the other, inserted at each end at the level of the ventral chætæ. Another point of difference there is, in that in Lumbricus these muscles do not traverse the body-cavity—they are embedded

[1] 'Arch. de Biol.,' x, 1890: "Rech. sur le syst. cutané et sur le syst. musculaire du Lombric terrestre."

in the longitudinal muscles of the body-wall. The "arciform muscles" are confined to those somites between the male pore on Somite xv and the hinder end of the clitellum at Somite xxxvii, and serve to produce during copulation the groove on the ventral surface, along which the spermatozoa travel from the male pore of one worm to the spermathecæ (?) of the other.

Now in Moniligaster, though we have no knowledge of the mode of copulation, yet there can be little doubt that these oblique muscles are connected with that process. By their contraction they would raise the ventral surface of the body between the male pores and the spermathecal pores, not, as I believe, for the passage of spermatozoa, but to help in holding the two worms together.

The minute structure of the prostate of M. Barwelli[1] has been dealt with by Beddard in more than one contribution; in one of these (4, p. 121, pl. xii, fig. 11) he figures a transverse section of this structure, and it will be convenient to refer to this briefly before passing to a consideration of what I find to be the condition in the present species. In M. Barwelli, then, the cavity of the prostate (or atrium) is lined by columnar granular cells; outside this is a layer of muscles; this, again, is surrounded by "an external covering composed of large granular cells, which are separated into groups by partitions. Each cell is prolonged into a fine process, which extends at least as far as the muscular wall; indeed, it is difficult to believe that the cells do not in some way or other reach the lumen of the atrium, and there discharge their glandular secretion."

In M. indicus the hemispherical glandular portion of the atrium, which portion may be termed the prostate, has a structure differing from that of the more compressed duct leading to the external aperture. The latter is provided with an irregular lumen, lined by a low columnar, non-glandular epithelium, the nuclei of which are oval and occupy the

[1] I shall use the word "prostate" to refer to the glandular wall of the organ, the word "atrium" being employed for the chamber into which the gland-cells and sperm-duct open.

middle of the cell (fig. 10); outside this is a thick coating of muscles in various directions, with of course numerous blood-vessels. But after a short course this simple epithelium gives way to a glandular coat (fig. 11), recalling the structure of the "prostate."

The "prostate" or glandular wall of the atrium (fig. 9), however, is lined by a layer of tall, thin, glandular cells, with nuclei (? at any rate deeply stained structures) placed at the sides of the cells, as if compressed; somewhat similar to, though much narrower than, the epithelium figured and described by Beddard.

The muscular coat, consisting of circular, longitudinal, and oblique fibres, does not immediately surround this epithelium as in M. Barwelli, but the two are separated by a considerable area, about twice as deep as the epithelium itself, which appears to be occupied partly by certain longer cells (*gl.*) than the lining epithelium, and partly by the necks of the extra-muscular multicellular glands (see figs. 8, 9).

In a foot-note on p. 573 of his memoir on Ocnerodrilus,[1] Beddard refers to the fact, as observed in M. Barwelli, that there is "hardly any distinction between a glandular and non-glandular section of the atrium." In the present species, as is shown, there is such a distinction very well marked.

Outside the muscular coat are the groups of glandular cells figured by Beddard. Each group (fig. 9) consists in a section of some eight to ten club-shaped cells, the narrow necks of which pass through the muscular coat, and can be traced in bundles nearly up to the epithelium. Each group is, in fact, a multicellular gland. This arrangement is quite evident in my sections, and the necks or ducts of the glands are quite noticeable, though I have been unable to trace the necks right up to the epithelium; the latter, however, is traversed by narrow clear tubes, resembling ducts, and which differ from the epithelial cells in having no inner boundary (as at *a*, fig. 9). The nucleus of each cell of the multicellular gland is naturally at the bottom, the widest part

[1] 'Trans. Roy. Soc. Edin.,' xxxvi, part 2.

of the cell. But I can give no detailed description of the finer histology owing to the ill-preservation of my material; I can detect granules, as if arranged around vacuoles, but very indistinctly. Outside the glands is a very delicate membrane (*cæ. ep.*), sparsely provided with flattened nuclei (*n. per.*), which I take to be the cœlomic epithelium, and which dips down, for some distance at any rate, between the groups of cells.

In Beddard's figure the muscular coat is made to be continuous, and no indication of "ducts" or communication between the gland-cells and the lumen is represented, though, as the above quotation shows, Beddard expected to find such "ducts." My description of M. indicus agrees pretty closely with Rosa's description of the prostate of M. Beddardii, and figure relating to the prostate of Desmogaster.

Beddard has already (4, p. 125) pointed out the resemblance between the gland (cement-drüse, prostate) attached to the atrium of Tubificidæ and the glandular lining of the atrium of Perichæta and other earthworms; at the same time he has denied the homology of the gland-cells of Moniligaster with those of Acanthodrilus, Perichæta, and other worms, chiefly, if not entirely, on the ground that in Moniligaster and in Rhynchelmis there is (according to his observations) no peritoneal membrane surrounding the glands; whilst the position of the gland-cells outside the muscular coat led him to regard these cells as representing the peritoneal membrane. Bnt I have seen what I believe to be the peritoneal membrane both in M. indicus and in Rhynchelmis; and further, the prolongation of the extra-muscular gland-cells up to the epithelium of the atrium in Moniligaster and Desmogaster seems to me to point conclusively to the derivation of those gland-cells from that epithelium, in the same way that the "cement-drüse" of Tubificidæ has been shown by Vejdovsky to be developed as an outgrowth from the lining of the atrium. Therefore probably the "prostate" of Tubifex is homologous with the "prostate" (using the word in a narrow sense to mean the glandular cells) of Moniligaster.

Telmatodrilus, Eisen,[1] one of the Tubificidæ, presents an intermediate condition between the arrangement met with in Tubifex and that in Moniligaster; for in this worm, instead of the single group of gland-cells communicating with the atrium, as in Tubifex and other of its allies, there are eight or ten such isolated groups (fig. 16, *b*) arranged around the upper part of the atrium, that is the "glandular part of the atrium," as I have called it in my description of Heterochæta.[2]

If now the atrium were to shrink, so to speak, these isolated groups of gland-cells would be approximated, and there would result a continuous coating of gland-cells, communicating here and there through the muscular coat with the cavity of the atrium, as we find in Moniligaster and Rhynchelmis.

In other earthworms, such as Acanthodrilus, Perichæta, &c., the structure of the prostate has been dealt with by Beddard (4); the chief difference from Moniligaster being, as I believe, due to the restriction of the muscular coat to the neck of the gland, and the consequently greater compression of gland-cells against one another (fig. 16, *e*).

In the "intermediate condition" (fig. 16, *d*) I have imagined the muscular coat becoming more definitely confined to the "duct," though some of the glands still perforate it; whilst others are in a condition similar to that in Deinodrilus, &c.

The spermatheca presents certain interesting features. The nearly spherical or slightly pyriform sac, lying above the œsophagus in Somite VIII, is provided with a very long delicate, shining duct,[3] several times coiled, which passes downwards to reach the body-wall in the anterior of the somite

[1] 'Report of Commissioner of Fish and Fisheries for 1883,' p. 880, pl. i, fig. 1.

[2] "Note on Aquatic Oligochæta," 'Quart. Journ. Micr. Sci.,' xxxiii.

[3] In M. japonicus Michaelsen mentions that he found only one "Samentasche" on the left side attached to the body-wall between Somites IX/X. If this is a spermatheca, it differs from the remaining species in being without the very characteristic long duct, as well as in its position.

in a line with the lateral chætæ (fig. 3). On dissection there appears to be an accessory gland in front and one behind the point of entrance of the duct into the body-wall, similar to that in many Perichæta and others; but in reality, as sections show, these two ovoid structures are due to the constriction, by Septum VII/VIII, of a single sac, with thick muscular walls, which opens externally in the intersegmental groove (figs. 5, 13, *cop. sac.*). This sac is lined by a columnar glandular epithelium, the nuclei of the cells being at their inner ends (fig. 14) similar to that of the spermatheca itself. The spermathecal duct perforates the dorsal wall of this sac at about its central point, where it is nipped by the septum, and owing to its cubical epithelium can readily be traced; the wall of the duct is very thick, being provided with a circular coat of muscles (fig. 15). It appears to me that possibly this sac is a copulatory sac in the true sense of the word, and that the muscular duct of the atrium is to some slight extent eversible, and is received into the copulatory sac.

Amongst the other species, in which the genital organs have been described, an arrangement at all comparable to this occurs only in M. Deshayesi. All recent authors agree that Perrier's interpretation of the organs lying in Somite VII as "prostates" connected with an anterior pair of testes is erroneous. Horst regarded these pyramidal glandular organs as "spermathecæ," the ducts of which unite to form a short common duct, receiving a more delicate "vas deferens" (Perrier). But Beddard has conjectured, rightly as it appears to me, that these glands are comparable to such accessories of the spermatheca as are usual amongst the Perichætidæ.

Perrier's fig. 79, pl. iv, represents a section through one of the pyramidal organs of Somite VII, which shows its glandular character, but an absence of muscle in its wall. In the present species the glandular lining is relatively thin, the muscular coat being very greatly developed. But in M. indicus no ducts such as Perrier figures exist. I would suggest that the wide bilobed sac in my worm corresponds to these pyramidal organs. In M. Deshayesi a greater differentiation has occurred, the

glandular portion being distinctly marked off from the muscular duct, whereas in M. indicus no such separation exists. If the bilobed structure of my worm were to be drawn out in such a way as to produce a couple of glands communicating by short ducts with a common duct, much the same arrangement would be produced.

The ovary closely resembles that represented by Rosa for M. Beddardii, and occupies the space between the displaced septum x/xi and that between Somite xi and xii, being therefore in Somite xi.

The oviduct is provided with a wide expanded funnel (fig. 8), very much as Perrier describes it; it is quite independent of the ovisac—that is, this latter structure opens into the cœlom outside the edge of the funnel, and not through it, as in some earthworms. Nor is there any reflected portion of the funnel entering the sac, as I have recently described in Sparganophilus.[1]

The ovisac is not so extensive as it is in several of the species, e.g. in M. minutus, A. G. B., where it traverses Somites xii—xv, but it is readily visible in dissection as a narrow white structure lying in Somite xii, and attached to its anterior septum.

The worm was not fully mature. I find no spermatozoa in the spermathecæ; those in the sperm-sacs are none of them fully formed, except some attached to the funnel of the duct. At first I took the muscular trabeculæ for spermatozoa, but by following their course from section to section I soon ascertained that this was not the case.

The ova in the ovary are quite small, and there are none in the ovisac.

I will now pass to the consideration of a few other points in the anatomy of M. indicus.

The Body-wall.—The usual muscular coats are present, but they show a feature which has hitherto not been noticed; the lateral regions both of the circular and the longitudinal layers are very much thicker than the dorsal and ventral

[1] "A British Aquatic Rhinodrilid," this Journal, November, 1892.

regions. In Plutellus Perrieri[1] I have noticed a somewhat similar thickening of the ventral body-wall, due, however, to the greater development of only the longitudinal coat. The longitudinal coat is, in Moniligaster indicus, interrupted by four continuous grooves, visible on simple dissection. It is in these grooves—marked *i. ch.* and *o. ch.* in fig. 7—that the chætophores are situated. On the ventral side of the lower groove is a special bundle of longitudinal muscles (*v. long. mus.*) which appears to run throughout the greater part of the worm, though I am not certain whether it extends forwards into the genital region, for I cut only longitudinal sections of this part. The longitudinal muscles exhibit a pinnate arrangement so well known in the group, but only in its thicker portions; it gradually merges into an irregular arrangement dorsally and ventrally (fig. 7).

In some of the anterior somites peculiar bundles of muscles traverse the body-cavity in an obliquely vertical direction, attached at one extremity just within the ventral chætophoral groove, and at the other to the outer part of the dorsal surface (fig. 6). These muscles I have referred to in speaking of the generative apparatus, and they are represented as seen in a dissected specimen in fig. 3. These oblique muscles are limited to Somites VII to X, for those which lie apparently in Somite XI, morphologically, as I believe, belong, like the atrium with which they are connected, to the preceding somite. I have referred above to the suggested purpose of these muscles.

The septa present the same variability in thickness which has been remarked in so many worms. In the present species the three septa, VI/VII, VII/VIII, VIII/IX, are thick and muscular, the remainder thin (figs. 3, 5). In other species of Moniligaster we find the same three, or an additional one in front thickened.

I believe none of the septa are absent, as Bourne states is the case for some of his species. Certainly on dissection

[1] "Description of Three New Species of Earthworm," 'Proc. Zool. Soc.,' 1892, p. 136.

some of the septa appear to have been lost; this is due to the peculiar shifting of the septa first pointed out by Horst and by Rosa.

The three thickened septa are nearly in their normal position, but are inserted in the body-wall slightly behind the intersegmental groove. The same is true for Septum IX/X, which is bagged out by the sperm-sac. Septum X/XI is, however, thrown back a whole somite; it is confluent with the Septum XI/XII along a certain part of its course laterally (fig. 5), but becomes separate towards the middle of the body, and is there inserted into the body-wall just in front of the groove XI/XII. At the level of the atrium, however, it can be traced below this organ to its insertion just behind the groove X/XI; that is, in a position corresponding to that of the preceding septa (fig. 8). The Septum XI/XII, again, is inserted in a normal position above the groove. There are, then, no septa absent in the present species.

Rosa's diagram of the arrangement in M. Beddardii shows it to be much less abnormal than in the present species.

In M. Houtenii, allowing for the fact that the various organs are situated one (testes, spermathecæ) or two (ovary, ovisacs) somites further back, the arrangement is the same; i. e. Septum X/XI is attached to body-wall about the middle of Somite XI, Septum XI/XII to the body-wall near the hinder part of Somite XII, Septum XII/XIII close to hinder boundary of Somite XIII and immediately in front of Septum XIII/XIV, which has almost the normal position.

Neither Beddard nor Michaelsen makes any remarks about this shifting of the septa, which may turn out to be a normal feature for the genus; and as it occurs too in Desmogaster, perhaps even for the family.

The nephridia closely agree with those of M. Houtenii; they commence in Somite IV, and are continued in each somite in a regular manner, and the fact that only one pair of nephridia occur in the wide stretch between Septum IX/X and that which I have referred to as Septum X/XI confirms me in this interpretation.

The nephridia in Somite IV are slightly larger than those immediately following, as Beddard has noted for M. Barwelli, the convoluted tube being thicker and whiter. I have not been able to assure myself as to the external opening, whether it is in the body-wall or in the stomodæal wall, but I believe the former.

The nephridia are provided, as in other species, with a very large muscular duct, forming a diverticulum. The coiled tube is embedded in tissue, as in Lumbricus, and a fairly extensive plexus of blood-vessels can be detected around the tube, as in all other "earthworms" except Ocnerodrilus, as opposed to "waterworms."

With regard to the vascular system I may merely state that the dorsal vessel is single, and is not accompanied by a supra-intestinal vessel. Four pairs of lateral hearts lie in Somites VI, VII, VIII, and IX; they are dilated and twisted, but are not moniliform. The lateral hearts in M. Deshayesi are in Somites VI, VIII, and IX; in M. Barwelli in VI—XIV.

In M. Houtenii the dorsal vessel is doubled as in Acanthodrilus, and hearts in Somites VI—XI. A subneural vessel exists, as Rosa has already stated; this has not yet been observed in any Microdrilid, but as it is frequently absent in Microchæta, Photodrilus, and others amongst the Macrodrili, no great stress can be laid upon its absence or presence.

The alimentary canal is constructed on the plan described by previous authors. The gizzards, of which there are four, lie in Somites XIII—XVI; they increase in size from before backwards, the fourth being nearly twice the width of the first (fig. 3); they are very distinct, but are not so deeply marked off from one another as Beddard figures (5, fig. 5) for M. Barwelli. Behind each gizzard is an annular fibrous band, apparently of connective tissue, for it appears white, and not glistening, as do the gizzards. Perrier and Horst mention them. Similar fibrous bands occur at the hinder end of Somites XI and XII in front of the septum, and the wall of the gut in Somite XII is distinctly more muscular than that of XI,

but very much less so than that of XIII, and not sufficiently muscular to be called a "gizzard." There is thus a transition between œsophagus and gizzard; and it may possibly be that the gut in these somites has been or is in near allies or varieties of this species more muscular than is the case with the single specimen which I have had the opportunity of examining; in fact, these regions may be potential gizzards. In other species the gizzards are either more or less extensive.

The position and extent of the gizzards appear to be one of the chief specific characters of the genus, and M. indicus differs from M. robustus, A. G. B., in this point, for in Bourne's species the gizzard occupies Somites XI—XV, presumably five in number; so that, as this is the only anatomical feature mentioned by Dr. Bourne, and notwithstanding the external resemblance with regard to the tail, I am justified in creating a new species.

There are no œsophageal glands nor other diverticula of the gut. In M. japonicus Michaelsen finds that the wall of the "œsophagus in Segments XV—XVIII (?)"—i. e. behind the gizzard—is much folded and very vascular. In the cavities of the folds he found a granular mass, which "must be regarded as concretions of carbonate of lime;" but he gives no evidence that this is the case. In none of the other species is any mention made of the presence of lime, though of course there is no reason why it should not occur.

The "tubular intestine" immediately behind the gizzard is narrow and cylindrical, remaining thus through Somites XVII to about XX. It then commences to enlarge till it attains its full diameter in about Somite XXX, where it occupies nearly the whole width of the cœlom. At each septum the "sacculated intestine" is very deeply constricted, so that quite a narrow neck connects the thin-walled dilated regions.

There is no typhlosole; the walls of the gut are very thin, and provided with a dense network of longitudinal and circularly disposed blood-vessels.

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EXPLANATION OF PLATE XXXII,

Illustrating Mr. W. Blaxland Benham's paper, "Description of a New Species of Moniligaster from India."

Figs. 1—15.—Moniligaster indicus.

Fig. 1.—The body-wall of six segments, cut through along the dorsal line and spread out. Viewed ventrally. × 5. *d.* Dorsal line. *v.* Ventral midline. *i. ch.* Inner series of chætæ. *o. ch.* Outer series. *neo.* nephridiopore. *spth.* Spermathecal pore. ♂. Male pore. ♀. Oviducal pore. *x.* Groove in front of male pore.

Fig. 2.—One of the chætæ.

Fig. 3.—A dissection of the left half of the animal, to illustrate the arrangement of the genital organs, and the position of the gizzards and the oblique muscles. Enlarged about 10 times. The somites are numbered, as also are some of the septa. Note the shifting of Septum x/xi. *cop. sac.* Bilobed copulatory sac, through which the spermathecal duct opens to exterior (see Fig. 5). *ann. band.* Annular bands between the gizzards. *giz.* 1, 2, 3, 4. The four gizzards. *obl. m.* Olique muscles (see Fig. 6) in certain of the somites. *o. ch.* Groove, due to interruption in longitudinal muscles throughout the body, along the line of the outer chætæ (a similar groove exists in connection with the inner chætæ). *œs.* Œsophagus. *ovd.* Funnel of oviduct. *sp. d.* Sperm-duct. *sp. sac.* Sperm-sac, lying in a pouch formed by Septum ix/x. *spth.* Spermatheca.

Fig. 4.—View of male organs on a smaller scale. The pouch of Septum ix/x is removed, and the sperm-sac (*sp. sac*) turned forwards, showing the greatly convoluted sperm-duct (*sp. d.*) lying in Somite ix. The spermiducal funnel is seen by transparency through the thin wall of the sperm-sac. *obl. m.* Oblique muscles attached to prostate, the duct of which is now seen. *o. ch.* The groove in line of outer chætæ.

Fig. 5.—A semi-diagrammatic longitudinal section through the genital somites. It is diagrammatic in so far as it shows both spermathecal pore and atriopore, the entire ovary, and other features which really exist in neighbouring sections. The external rings are labelled with Roman numerals, the cavities of the somites with Arabic numerals; the septa are lettered. *at. o.* Male pore, or atriopore. *circ.* Circular muscles of the body-wall. *cop. sac.* Copulatory sac, showing entrance of spermathecal duct. *lg. m.* Longitudinal muscles of the body-wall. *neph.* Portions of nephridial tube. *neph. bl.* Cæcal bladder of nephridium. *obl. mus.* Oblique muscles cut across. *sp. d. o.* Aperture of sperm-duct into atrial cavity; its course is shown from the septum, backwards in the longitudinal muscles of body-wall, and through the prostate. *sp. funnel.* Funnel of sperm-duct, which does not actually occur in the same section as the testis. *spoa.* Spermatozoa in sperm-sac; some are seen attached to funnel. *spth.* Spermatheca. *spth. d.* Spermathecal duct. *spth. o.* Aperture of spermatheca.

Fig. 6.—Diagrammatic transverse section through half the body in anterior region, to show position of oblique muscles. *i. ch.* Groove, along which are inserted the inner chætæ. *o. ch.* Similar groove for outer chætæ. *n. c.* Nerve-cord. *sub. n. v.* Subneural vessel.

Fig. 7.—Half a transverse section through the intestinal region, in order to show the peculiar band of longitudinal muscle (*v. long. mus.*) which traverses this region of the body. The lateral thickening of the body-wall is also seen in these two sections.

Fig. 8.—A longitudinal section of the atrium and neighbouring parts. The Septum x/xi is seen passing forwards underneath the atrium to be inserted near anterior boundary of the somite (cf. Fig. 5) where this septum coalesces with Septum xi/xii. *circ. m.* Circular muscles of the body-wall. *cœ. ep.* Cœlomic epithelium outside the prostate. *gl.* The glandular region of the duct of the atrium. *long. m.* Longitudinal muscles of the body-wall, a portion of which is continuous with the muscular wall of the atrial duct. *multicell. gl.* Pyriform groups of gland-cells projecting outside the muscular coat (*mus. coat*) of the atrium, and whose necks traverse this coat. *neph.* Portion of nephridium in Somite xi. *obl. m.* Oblique muscles, some amongst the longitudinal and others amongst the muscles of the atrial wall. *ov.* Portion of ovary. *ovd.* Edge of the funnel of the oviduct. *p.* Prominence of the lining of the atrium, on the apex of which (in another section) the sperm-duct opens. *sp. d.* Portion of sperm-duct in the wall of the atrium.

Fig. 9.—A portion of the prostate (wall of the atrium) greatly magnified. One group of gland-cells is represented in detail; the necks of the cells are readily traced through the muscular coat (*mus.*), but not so readily traced up to the epithelium (*ep.*). The latter is, however, traversed by narrow ducts (as at *a*), which are, no doubt, the necks of the gland-cells. Between the epithelium and the muscular coat are large pyriform glands, the details of which could not be made out owing to the preservation of the material. *b. v.* Blood-vessels. *n. per.* Nucleus of flat cœlomic epithelial cells, which surround the multicellular glands and dip inwards between them.

Fig. 10.—A portion of the epithelium of the atrial duct. *m.* Muscles. *b. v.* Blood-vessel.

Fig. 11.—A portion of the glandular region of the atrial duct (see Fig. 8, *gl.*). *ep.* Epithelium. *gl.* Gland-cells. *m.* Muscles.

Fig. 12.—Transverse section of sperm-duct. *ep.* Large striated epithelial cells. *mus.* Muscles. *spoa.* Spermatozoa.

Fig. 13.—Longitudinal section of the copulatory sac, showing its constriction by Septum vii/viii, and the entrance into it of the spermathecal duct (*spth. duct*). *ep.* Epithelium. *mus.* Muscular coat.

Fig. 14.—A portion of the epithelium of the copulatory sac.

Fig. 15.—Section of spermathecal duct, to show the very thick coat of circularly disposed muscles.

Fig. 16.—A series of diagrammatic sections illustrating my view as to the development of the prostate in earthworms from the condition in Tubifex. The lining epithelium of the atrium is represented as consisting of cubical cells, the muscular coat by thick lines, the cœlomic epithelium by interrupted lines.

Fig. 1.

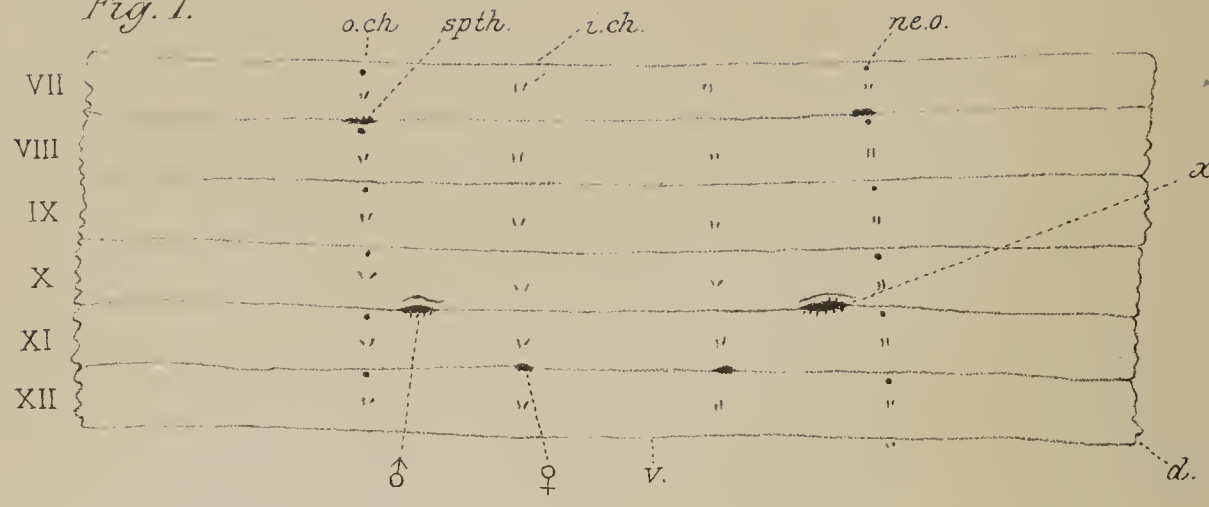
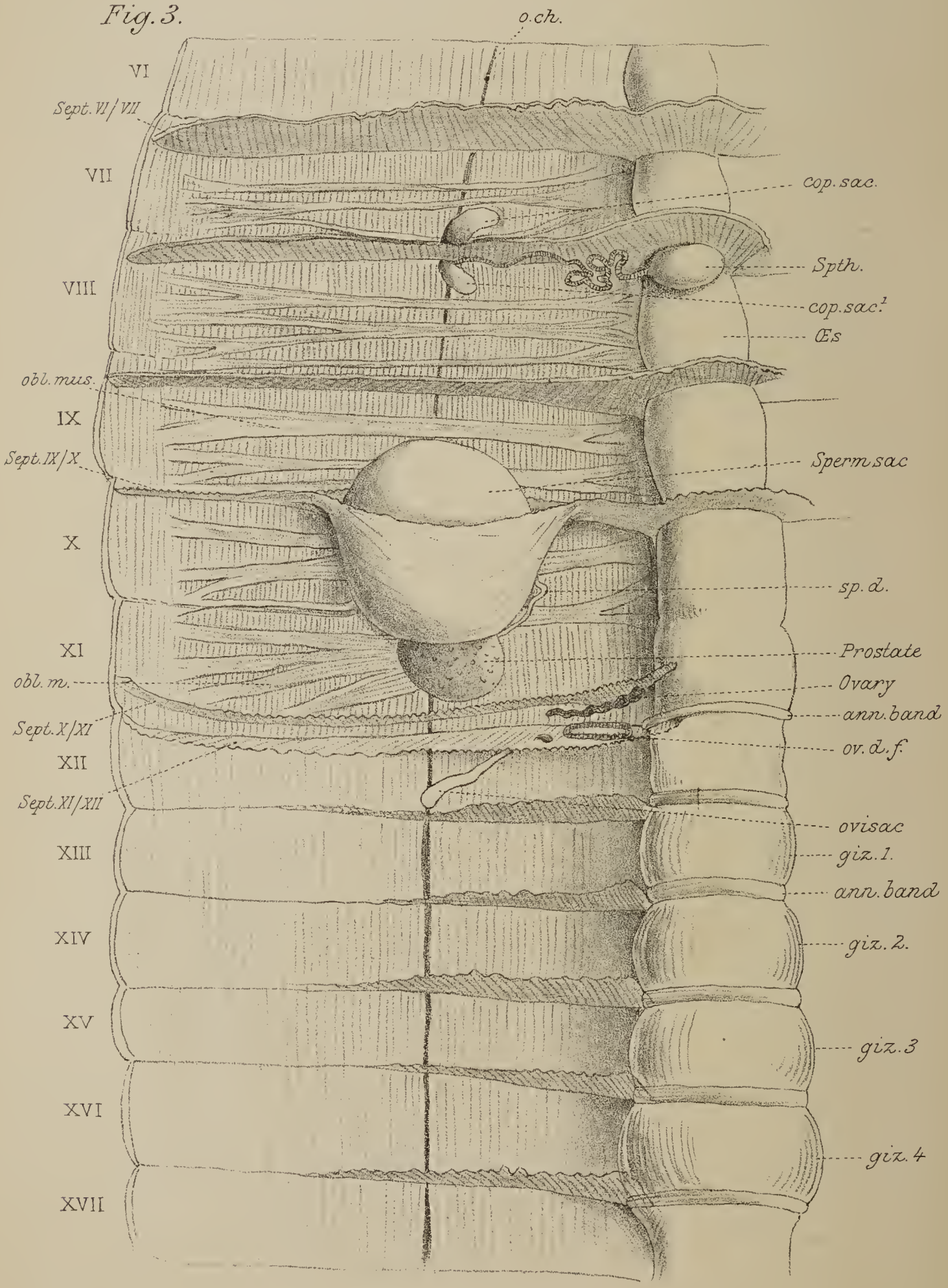


Fig. 2.

Fig. 3.



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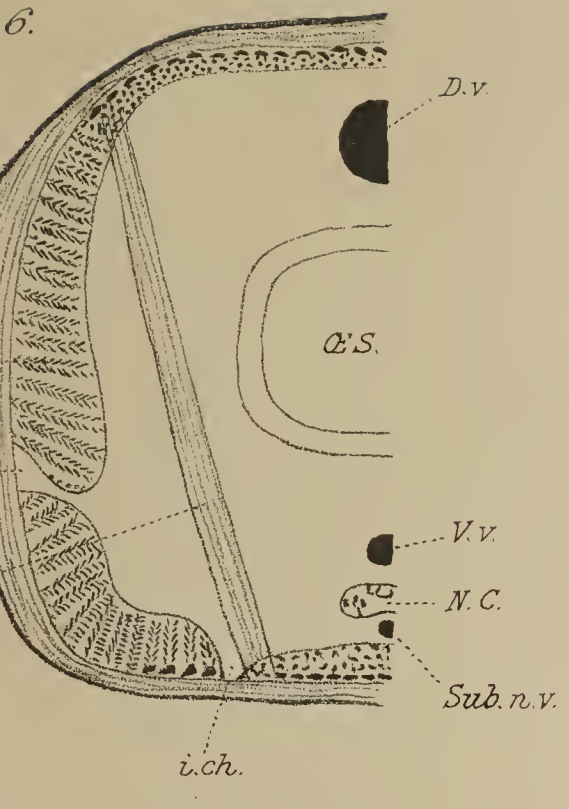

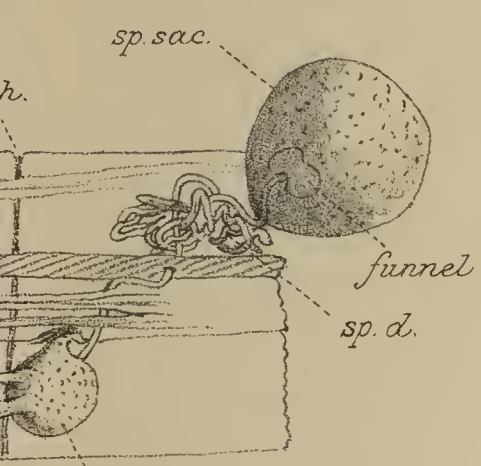

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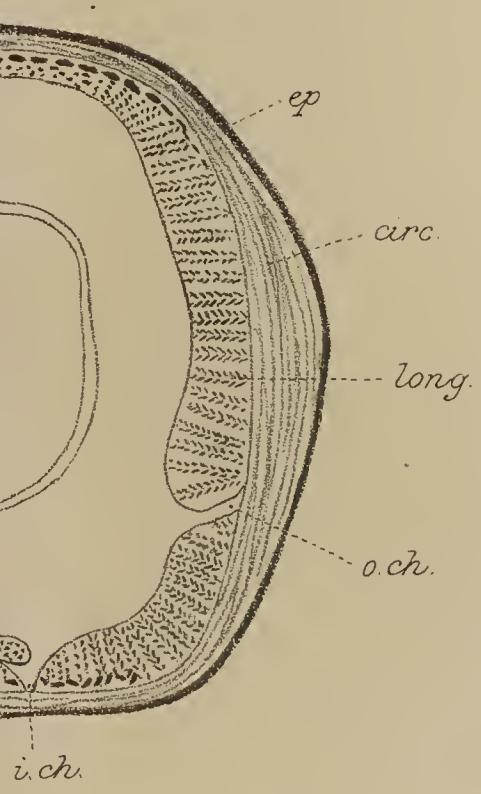
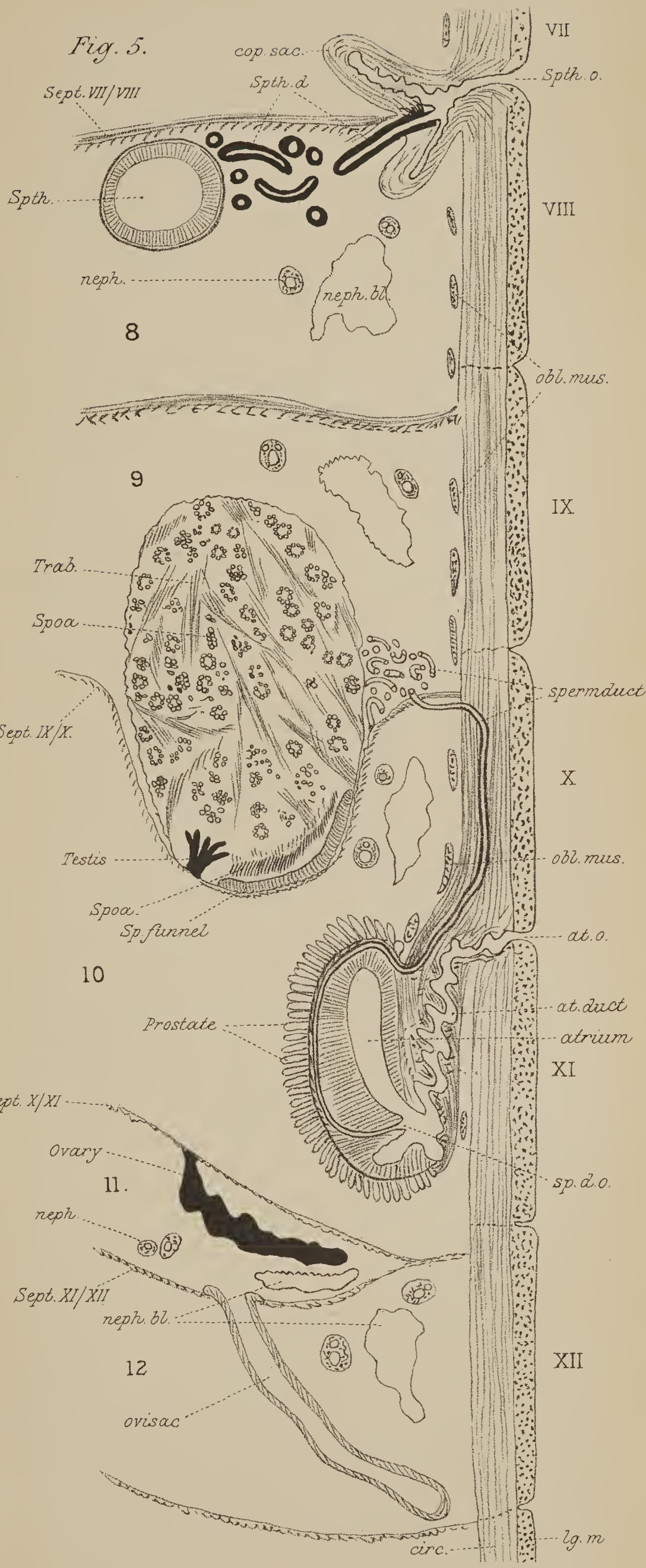


Fig. 5.



F.Huth, Lith^r Edin^r

Fig. 8.

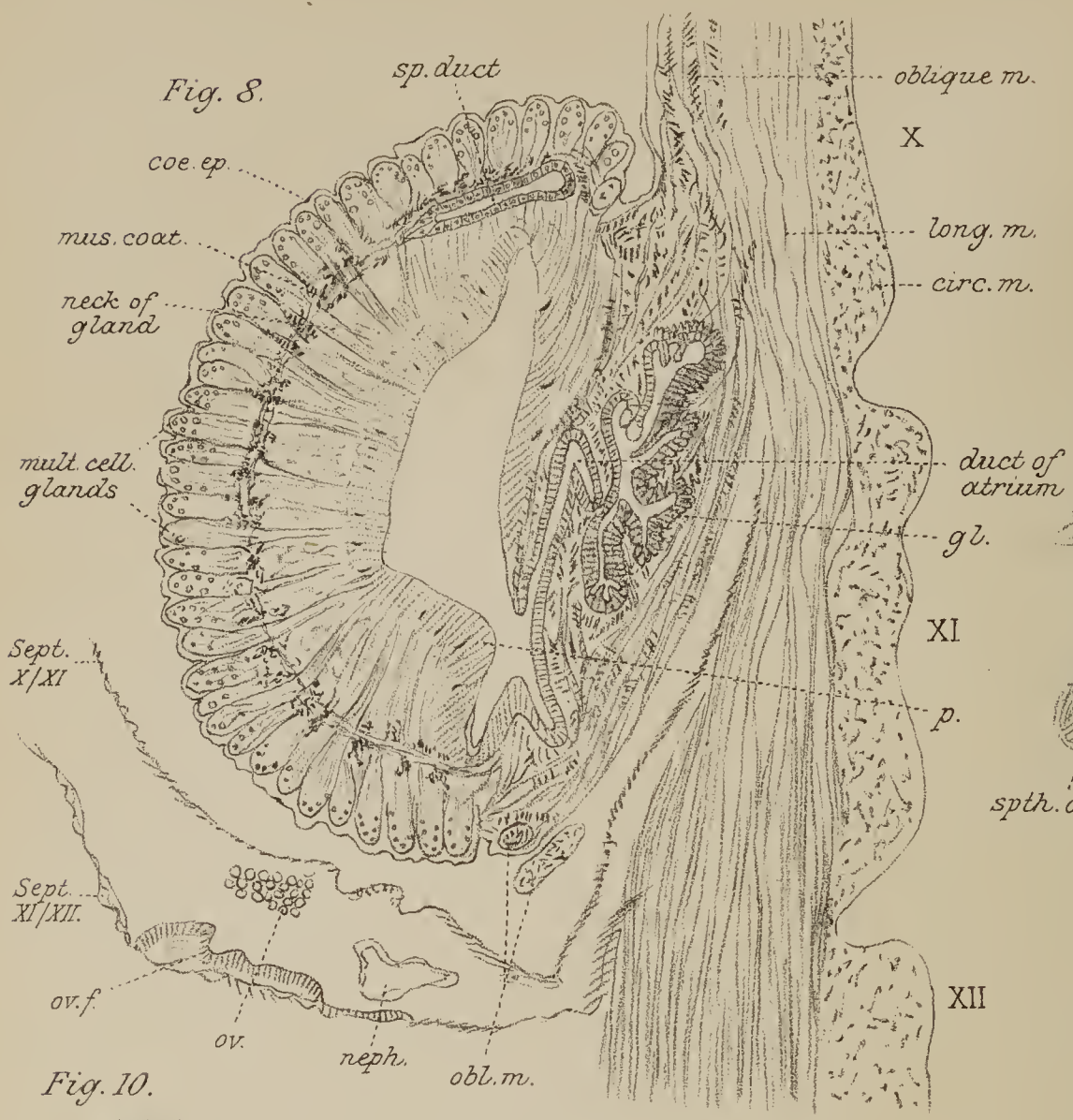


Fig. 10.

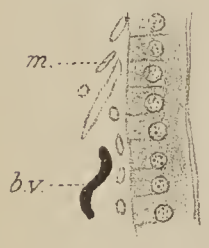


Fig. 11.

Fig. 14.

Fig. 12.

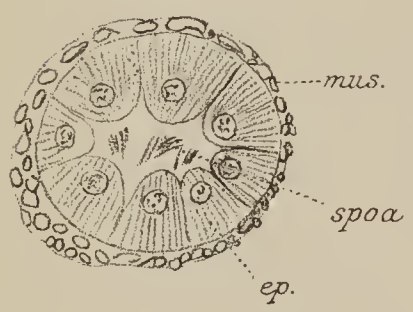


Fig. 15.

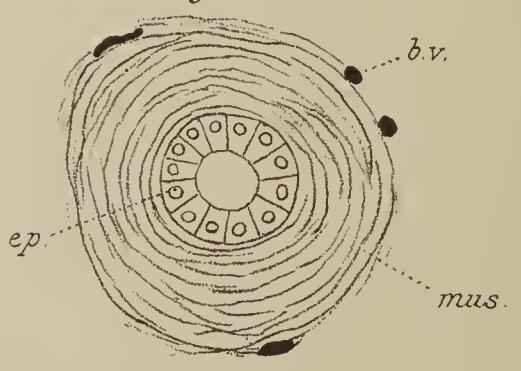


Fig. 9.

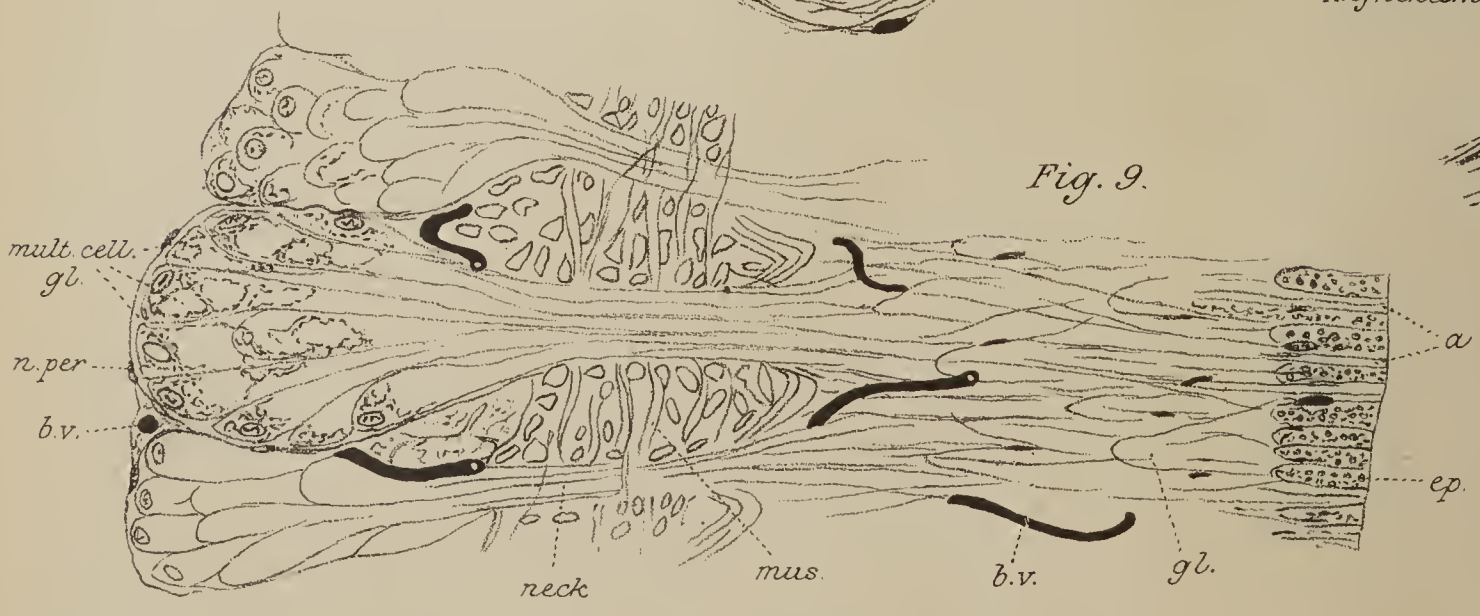
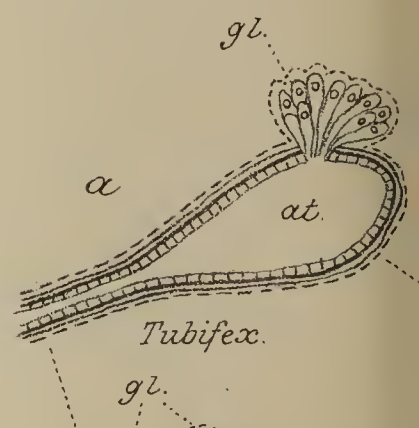
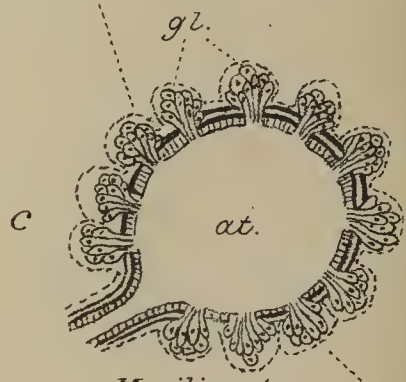


Fig. 13.



Tubifex.



Moniligaster.
Rhynchelmis.

W. B. Benham del.

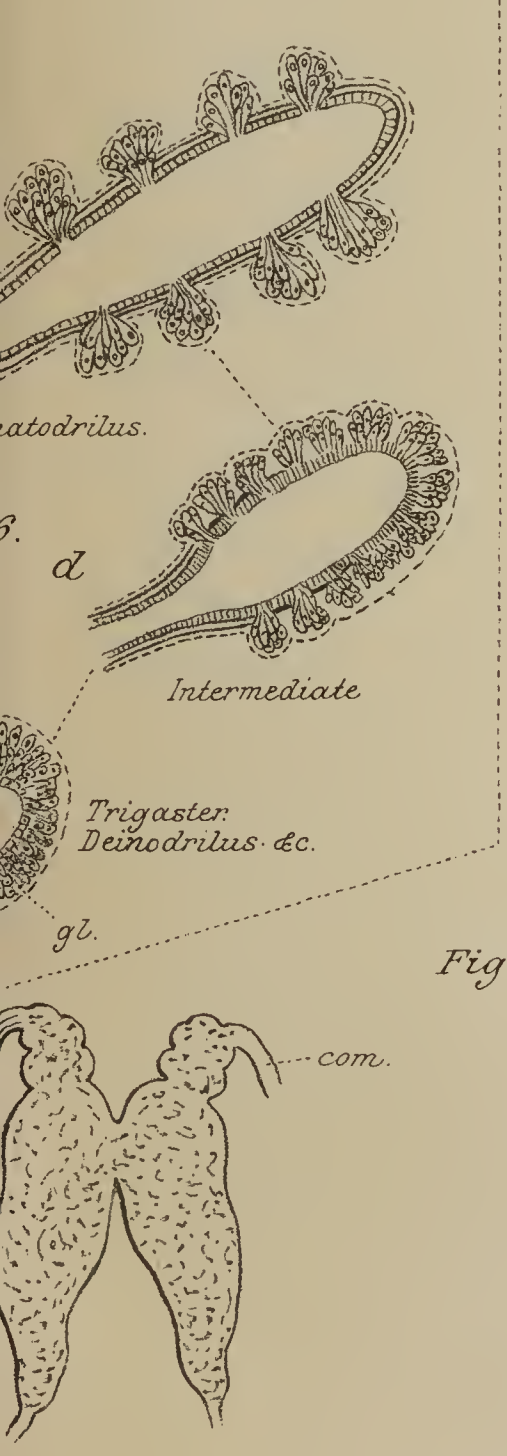


Fig. 2.

Fig. 4.

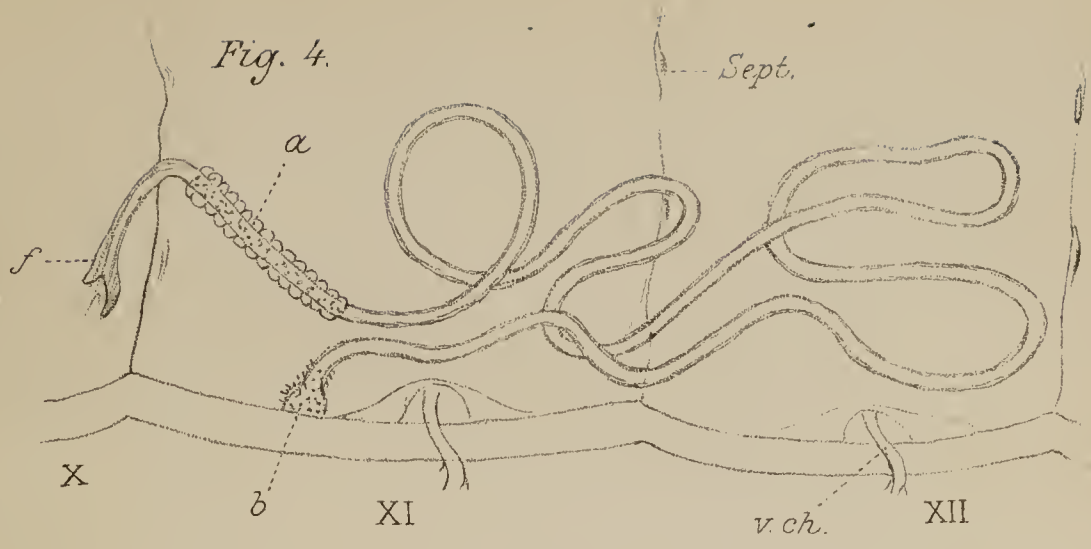
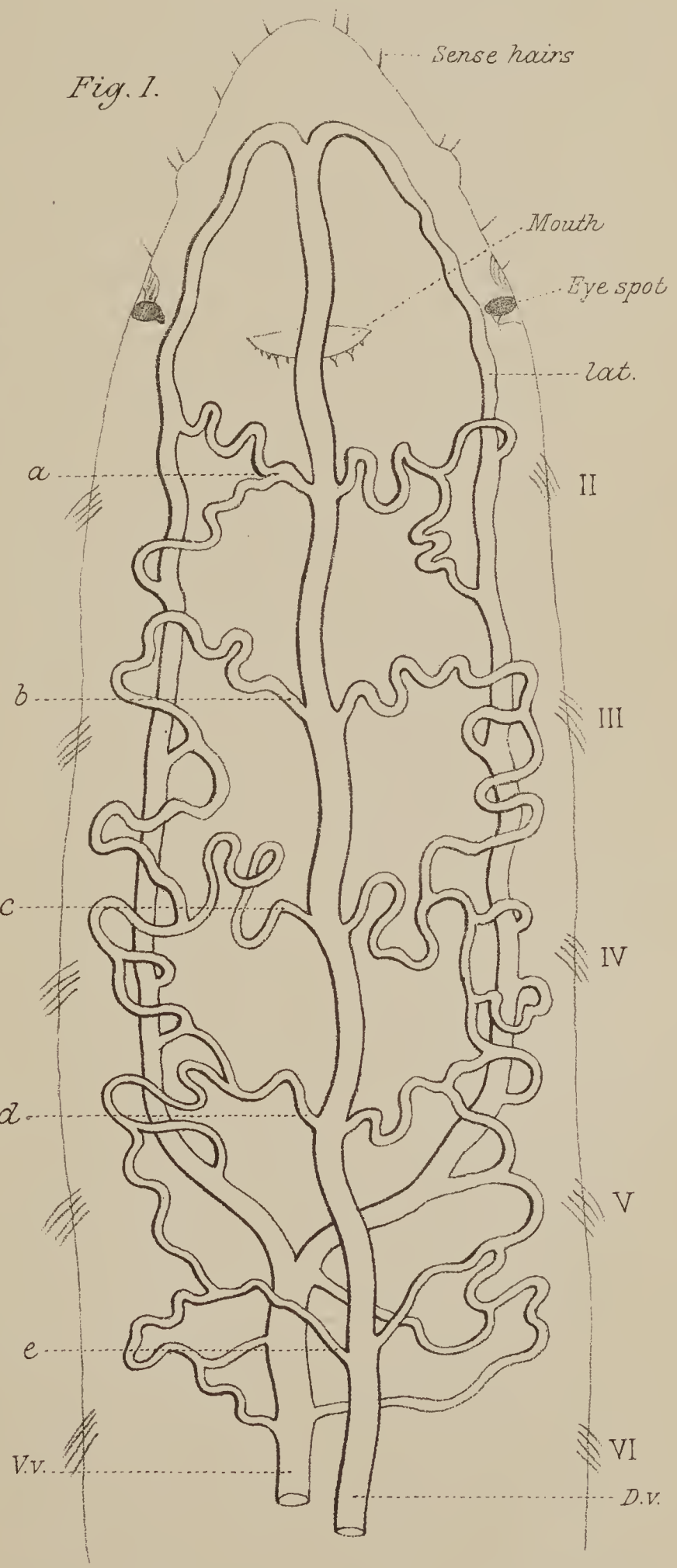


Fig. 3.

Fig. 1.



Figs 1–5. NAIS HETEROCHŒTA, n. sp.

F. Huth, Lith.r Edin.r

Note on a New Species of the Genus Nais.

By

W. Blaxland Benham, D.Sc.Lond.,
Aldrichian Demonstrator of Comparative Anatomy in the University of Oxford.

With Plate XXXIII.

In a gathering from a ditch in the neighbourhood of Oxford I found several specimens of a species of Nais, which present features differing from those recorded for any species of which I have been able to find a recognisable description.

Nais heterochæta, n. sp., is a small worm about a quarter of an inch in length, of a dull brownish colour. I have not yet come across any sexually mature forms, or specimens exhibiting zones of budding; the number of somites varies from about thirty-one to about forty-one in specimens which I have observed from this point of view.

The dorsal bundles of chætæ have a characteristic composition, which the specific name is intended to indicate. Normally there are only two chætæ to a bundle—cases with three being very rare. These two chætæ are of different shape and size. (*a*) One is capilliform, but comparatively short, being ·165 mm. in length, not as long as the body is broad; (*b*) is a small furcate or "crochet," measuring ·045 mm. (fig. 2).

The length of the capilliform chætæ varies slightly in different regions of the body; those of the Somites VI and VII being shorter than the above length, and those of Somite XII exceeding it to a slight extent. They gradually increase in

length then up to Somite XII, then decrease for a few somites, and retain a normal length to the end of the body. In one or two specimens I noted that the dorsal chætæ of Somite VI consisted only of crochets, one on one side, two on the other side; in Somite VII there were two furcates and a short capilliform, only slightly exceeding them in length. It is, perhaps, needless to remark that the dorsal bundles are absent in the first five somites.

A comparison of my figure of these dorsal chætæ with those of Vejdovsky[1] shows that the shape of the chætæ does not agree with those of either of the species, N. barbata, N. elinguis, or N. josinæ, described by him.

In the last species, however, the dorsal bundles do contain crochets in addition to capilliforms; but not only do these differ from those of N. heterochæta in position of the "node," but also in the fact that two of them and two capilliform exist in a bundle, and in the relative size of the two.

Another point of difference—if the above be not sufficient—is the presence of eyes in my species, whereas they are absent in N. josinæ.

The ventral chætæ (fig. 3) are of the usual Naid shape; usually there are four in a bundle, rarely three or five. Those of Somites II, III, IV, and V differ slightly from the remainder in that the distal prong is rather longer than the proximal; whilst in the normal chætæ the two prongs are, as nearly as I can make out, equal in length, though the proximal prong is distinctly the stronger.

The blood is yellow, and the connections between the dorsal and ventral trunks (fig. 1) are peculiar. The two lateral branches into which the dorsal vessel divides in the prostomium, in front of the brain, unite in Somite V to form the ventral trunk; these are connected with the dorsal trunk by four pairs of vessels, each of which branches more or less irregularly, as will be understood better by a reference to the figure than by a description.[2] The arrangement is

[1] 'System und Morphologie d. Oligochäten,' pl. ii, figs. 18, 19, 26.

[2] These branches are accompanied by irregular patches of brown pigment

less regular than in N. elinguis, or Bohemilla, or Paranais, but more regular than in N. josinæ. One very peculiar feature, hitherto unrecorded, I believe, is the connection which exists between the branch *d*, in Somite v, and the "commissural" vessel *e* in Somite vi, which connects the dorsal and ventral trunks; the branching of this commissural vessel is also peculiar. The shape of the brain is utilised by Vejdovsky for determining species, therefore I have appended a figure of this organ in N. heterochæta (fig. 5); it will be seen to resemble somewhat the brain of N. josinæ (Vej., Taf. ii, fig. 28) in the constriction of the anterior lobes from the posterior, but in N. heterochæta this is more marked, and at the same time the shape of the posterior lobes is different.

With regard to the gut, the "stomach," or dilatation in Somite viii, is not nearly as marked as in other species, and more nearly resembles that in Paranais littoralis.[1]

The pigmented covering of chloragogic cells commences in Somite vi, and is continuous thence throughout the body till quite near the posterior end.

The nephridia present the peculiarity which has scarcely been sufficiently insisted upon by recent writers, though it has been recorded by Carter[2] and by Timm,[3] that very usually there is in Naids only a single nephridium in some or all the somites. In the present species there is never more than one nephridium per somite; the nephridium is very long, and frequently the coiling tube occupies two somites, communicating by means of a funnel with a third somite (fig. 4). In this case, then, there is one nephridium in the place of four (a pair in Somite xi and a pair in Somite xii). In most of the somites the nephridium lies on the animal's right side. So far as I have been able to observe, in the living animal there

[1] See A. G. Bourne, "Notes on Naidiform Oligochæta," 'Quart. Journ. Micr. Sci.,' xxxii, Pl. XXVI, fig. 2.

[2] "Spermatology of New Species of Nais," 'Ann. Mag. Nat. Hist.,' ii, 1858, p. 1.

[3] "Beob. üb. Phreoryctes und Nais," 'Arb. aus Zool. Inst. Wurzburg,' vi, 1883.

is no trace of the other nephridia. It will be an interesting point to look for in the developmental history of the genus—the suppression of nephridia; for Michaelsen has described certain earthworms, Kynotus, in which the nephridia are stated to occur in alternate somites. I have suggested elsewhere that an error in observation may perhaps have occurred, and that the external markings indicating "somites" are in reality annuli. But in Naid, of course, there is no question of annuli.

The first nephridium lies in Somite VII; the arrangement in following somites is subject to a good deal of variation.

The post-septal glandular region of the tube is of a different shape from that figured by Vejdovsky for N. elinguis, and more nearly resembles therein N. josinæ (Vej., pl. iii, fig. 4, *a*); but with regard to the terminal dilatation this species differs considerably from N. heterochæta (cf. my fig. 4).

EXPLANATION OF PLATE XXXIII,

Illustrating Mr. W. Blaxland Benham's "Note on a New Species of the Genus Nais."

FIGS. 1—5 illustrate specific characters of Nais heterochæta, n. sp.

FIG. 1.—The vascular system of the anterior somites. *D. v.* Dorsal trunk. *lat.* The two branches from the dorsal trunk which unite to form the ventral trunk (*V. v.*). *a*, *b*, *c*, *d*. Vessels more or less branched, passing from dorsal to lateral vessel. *e*. A commissural vessel from dorsal to ventral trunk, also branched.

FIG. 2.—A dorsal bundle of chætæ, consisting of one capilliform and one furcate chæta.

FIG. 3.—A ventral chæta.

FIG. 4.—A nephridium, showing its extension into two somites. *sept.* Septum. *a*. Granular post-septal region. *b*. Muscular (?) duct. *f*. Funnel.

FIG. 5.—Brain. *com.* Origin of œsophageal commissure.

On a New Organ in the Lycoridea, and on the Nephridium in Nereis diversicolor, O. F. Müll.

By

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Assistant to the Linacre Professor of Human and Comparative Anatomy, Oxford.

With Plates XXXIV & XXXV.

About two years ago, while examining some sections of a Nereis (probably N. diversicolor, O. F. Müll.) which I had cut in the Zoological Laboratory at University College, London, I discovered an interesting organ, which appears to have hitherto escaped the notice of those naturalists who have studied the anatomy of the Nereids. Since then I have from time to time continued my observations, both in London and in the Oxford Museum, always hoping to be able to obtain the stages in the development of Nereis, the study of which alone can give a real clue to the homology and functions of these organs. This unfortunately has not been possible, owing chiefly to the fact that I have not been able to go myself to the sea-side to pursue my researches. It has therefore been thought advisable to publish the facts as they stand, and this paper amounts to little more than a mere description of this new organ. Some notes on the minute structure of the nephridium of the Nereids have also been added.

Various genera and species were examined, but most of the observations were made on Nereis diversicolor, which occurs in abundance at Plymouth, whence I have obtained

my specimens alive. A detailed description will, therefore, be first given of the organ in this species, which will then be compared with some other members of the family.

If the fresh worm be killed, laid out, and slit up on the dorsal surface on each side along the bases of the parapodia, and a piece of the strip so obtained be placed with the inner surface upwards on a slide and examined under the microscope, there will be seen running transversely on either side, and curving round the outer edge of the great longitudinal muscles, faint lines made by a folded area of the cœlomic epithelium, bounded in front by a lateral blood-vessel coming from the dorsal vessel. This folded and thickened patch of epithelium extends over the dorsal longitudinal muscles in the posterior half of each segment, and its surface is covered with delicate cilia. If now the strip be examined from the upper surface the folded ciliated area is seen to extend transversely across the middle of each segment, becoming narrower and narrower, and reaching to near the mid-dorsal line. I propose to call this organ the dorsal ciliated organ until we know more about its functions; the portion which lies on the outer surface of the muscles may be called the outer limb, and the portion which lies on the inside of the muscles the inner limb. Little more can be seen in the fresh condition; the exact position and structure of the organ can only be ascertained by means of sections.

For the preservation of Nereis diversicolor hot corrosive has, on the whole, given the best results. The worms were chloroformed, then opened up here and there, and the hot preservative poured on them. Hæmatoxylin and borax carmine were used as stains.

In a transverse section through the middle of a segment of an adult N. diversicolor (Pl. XXXIV, fig. 5) we see a covering of ciliated epithelium extending on the outer surface of the dorsal longitudinal muscle (figs. 1 and 5, *dors. long. m.*), and round its ventral border on to the lateral tegumentary blood-vessel (figs. 1 and 5, *dors. teg. v.*) which communicates with the dorsal vessel (figs. 1 and 5, *dors. v.*). This is the outer limb of the

dorsal ciliated organ (Pl. XXXIV, figs. 1, 2, 5, *o. limb* ; Pl. XXXV, figs. 15, 17, *o. limb*). Fig. 15 represents a transverse section through the dorsal muscle of another specimen, taken rather farther back in the segment than that in fig. 5, thus avoiding the blood-vessel. The ciliated organ curls round the edge of the muscle, and ascends on its inner side nearly as high as the slight angle formed where this muscle leaves the body-wall. It will be seen that the inner limb (fig. 1, and figs. 15, 17, *i. limb*) does not adhere closely to the muscle, but to a fold of the septum which is bounded anteriorly by the dorsal tegumentary vessel (figs. 1, 4, 15, 17). The septum, in fact, is not attached to the inner face of the longitudinal muscle, and its free edge bends forward at right angles (fig. 4, *fl. sept.*), and proceeds upwards, leaving a space between itself and the muscle (figs. 1, 4, 5, 15, 17) ; it is on the inner side of this flap, which faces slightly backwards, that is situated the inner limb of the dorsal ciliated organ (figs. 1, 4, 5, and figs. 15, 17, *i. limb*). The outer and dorsal limb varies somewhat in its extension, sometimes reaching quite near the median dorsal line, as I have already mentioned. In this region blind prolongations of the cœlom run up between the longitudinal muscles and the body-wall (figs. 1, 5, 7, *dors. cœl.*) ; they are separated from each other by connective-tissue walls. Small blood-vessels (fig. 7, *bl. ves.*) and bundles of circular muscle-fibres run along the cœlomic spaces (fig. 7, *circ. m.*). The end of the outer limb of the dorsal ciliated organ (fig. 7, *o. limb*) extends up the largest of these spaces (which is situated almost exactly in the middle of each segment), being continuous with the cœlomic epithelium which lines the space and covers its anterior side. A branch of the tegumentary vessel follows it closely during its course. I first expected that this dorsal tubular prolongation of the cœlom would, with the outer limb of the ciliated organ, lead to an external aperture ; but I have looked in vain for such a pore in numerous sections—transverse, sagittal, and horizontal. Both cœlomic space and ciliated organ gradually dwindle away until they disappear altogether some little way from the median

dorsal line. As for the extension of the organ at its ventral border, fig. 4, which represents the middle portion of the sagittal section through two segments, shows that it reaches halfway across the segment from near its posterior limit (figs. 2, 4, *dors. cil. org.*). The surface of the organ is much folded, especially the outer limb.

The finer structure is shown in figs. 4 and 6. In the former, which was taken from a section stained in borax carmine, the cells are seen to have indistinct walls and to be somewhat striated on the outer edge, which is very darkly staining. The nuclei are large and more or less oval in shape. Fig. 6 represents a small portion of the organ, taken from a section very similar to the right side of that shown in fig. 5. This section has been stained with hæmatoxylin, and shows no distinct cell outlines. The protoplasm in which the nuclei are embedded is slightly granular within, and under a high power (Z. 2 mm. hom. oil im. and oc. 8) appears to be divided up into chambers, as it were, by the minutest ramifications of a network of darkly staining substance very similar to that described below in the nephridium. Towards the inside this substance forms the thin limiting membrane (Pl. XXXIV, fig. 6, *l. mb.*) which lies on the muscle, while towards the free surface it forms a dark zone (fig. 6, *d. z.*), and then the dark lines which give the outer edge of the organ its striated appearance. Outside this striated layer, at the very surface, the darkly staining substance forms a cuticular layer (fig. 6, *cut.*). The surface is beset with fine cilia (fig. 6, *cil.*), the bases of which, perhaps, are continuous with the light portions of the striæ in the underlying substance. On every side the epithelium forming the organ is continuous with the cœlomic epithelium, of which it is, in the adult at all events, a highly modified patch. It is quite clear from these descriptions, I think, that the dorsal ciliated organ shows no trace of a glandular structure.

In conclusion, I may say that this organ is present in every segment of the body from the tenth, except the last two, in which the nephridia appear to be also absent. It occurs in both sexes, and I have found it in every member of the family which

I have had the opportunity of examining—namely, Nereis diversicolor, N. macropus, Clp.,[1] N. cultrifera, Gr., Alitta virens, Sars, and Nereilepas fucata, Sav. In all these species the organ resembles that described in N. diversicolor in every particular, as far as I was able to ascertain; but in some cases the specimens were not very well preserved. It is a somewhat remarkable fact that I have failed to find it in two Heteronereid forms (the ♀ Heteronereid of N. pelagica, and a small ♂ Heteronereid which I have not yet been able to identify).

Of other genera, both nearly related to, and far removed from, the Lycoridea, I have examined the following species: Aricia fœtida, Nephthys scolopendroides, Eunice sp., Lumbriconereis impatiens, Staurocephalus Rudolphii, Sthenelais dendrolepis, Polynoë elegans, Rhynchobolus convolutus, and R. siphonostoma. In none of these forms has any trace of the dorsal ciliated organ been found, and it is to be noticed that all these species have nephridia provided with large and widely open funnels, and short, more or less straight, ducts.[2]

A short time ago Professor Lankester directed my attention to a very interesting paper by Professor A. Kowalevsky (7) on excretory organs, in which certain segmentally arranged organs, occurring in N. cultrifera, are shortly described. I shall quote the passage in full from p. 71: "Das Indigokarmin [which the animals had taken in] wird meistens von den Blutkörperchen aufgenommen, und zum Teil färbt es in jedem Segmente besondere Organe, welche an der Ruckenseite der Segmente liegen und aus drüsenartigen Zellen der Haut bestehen, unter denen man immer eine grosse Anhäufung der Blutkörperchen sieht. Die Stellen, welche so das Indigokarmin bei Nereis aufspeichern, sind auch an normalen Tieren zu sehen; dies sind Stellen mit Anhäufungen von braunen

[1] I am much indebted to Signor Lo Bianco, of the Naples Zool. Station, for collecting and sending me several species of Nereis.

[2] I hope soon to be able to give a description of the minute structure of the nephridia of some of the genera mentioned above.

oder gelben Körpern, die in jedem Segmente und besonders in den hintern liegen. Diese Stellen nun speichern auch das Indigokarmin auf. Tötet man mit Alkohol eine so bearbeitete Nereide und spannt sie dann auf oder nimmt nur die Haut der Rückenseite, so gewinnt man ein Präparat wo diese blauen Organe in jedem Segmente sich metamerisch wilderholen und den Eindruck besonderer regelmässiger Segmentarbildung machen." It seems evident that this excretory organ is not the same as the dorsal organ I have described, which is not glandular, and is not situated in the skin. Also Kowalevsky makes no mention of cilia. On the other hand, it appears not improbable that the "grosse Anhäufungen der Blutkörperchen" seen below the excretory organ are the accumulations of cœlomic corpuscles, which seem to be collected together by the cilia of the dorsal organ near the top of the outer limb (Pl. XXXIV, figs. 5, 7, *cœl. corp.*); it also frequently happens that a large number of ova are collected in this region.

When I first discovered the dorsal ciliated organ in Nereis, I was immediately struck with its remarkable resemblance to the genital ducts (Genitalschläuche) described in the Capitellids in Dr. Eisig's beautiful monograph (6). I have obtained sections of Nereis showing the organ in question almost exactly like Eisig's figs. 1, 2, and 14, pl. xiv. It seems to me, therefore, very likely that we have here a "genital duct," which has not yet acquired an opening to the exterior. My inability to show such an opening may, perhaps, be explained by the fact that it has never been my good fortune to obtain a perfectly mature Nereid. The acquiring at maturity by the duct of an opening would be a fact by no means unparalleled in nature; in the Capitellids themselves it only occurs late (6). It may be remarked, also, that the dorsal organ of Nereis and the genital ducts of the Capitellids show many points of resemblance in histological detail.

Mr. Cunningham (4) argues that it would be quite impossible for the genital products in Nereids to be discharged by means of the nephridia; in this I entirely agree with him. Not only would it be impossible for the ova to escape by the

nephridial canal, owing to their size; but their nuclei alone could not pass down its tortuous and narrow lumen. The genital products must therefore escape either by dehiscence, as held by Mr. Cunningham (4), or by means of genital ducts (ducts such as we know to be formed at maturity in the Nemertines).[1] The former method would be neither agreeable nor advantageous to the parent; the latter, on the contrary, would seem to be the natural one.

The fact that no dorsal organs were found in the two Heteronereids I have examined, does not appear unnatural when we consider that these forms are much modified for the purpose of dispersing the ova, and are in many respects degenerate and unfitted for a long life.[2] Probably, in this case, dehiscence takes place, followed by the death of the individual.

The Nephridia.

Although many naturalists have examined the nephridia of various members of the family Lycoridea, these organs are still but incompletely known.

One of the chief difficulties we meet with in studying the nephridia of the Nereids, is owing to the small size of most of these worms (except Alitta virens and Nereis pelagica, which unfortunately I have not been able to obtain alive). However, if a N. diversicolor be carefully dissected under a powerful lens, the nephridia may sometimes be seen as small yellowish or whitish bodies at the base of each parapodium. On removing these with the septa, the whole organ, both body and funnel, may occasionally be obtained. It is then seen to consist, as described by Mr. Cunningham (4), of an opaque, massive body, containing a convoluted tube, which leads to a long canal terminating by a small funnel, the internal opening.

[1] Should future observations establish the fact that the dorsal ciliated organ is a genital duct, it might well be compared with the metameric genital canals of the Nemertines.

[2] Not only is the alimentary canal much reduced (according to Claparède [2] the Heteronereids take no food), but the nephridia also seem to be degenerate and in some cases even absent. I have not, however, yet been able to examine sufficient material to say anything definite on this latter point.

The whole nephridium is covered with cœlomic epithelium. I have not attempted to follow out the complicated coils of the nephridial tube in series of sections; but fig. 8, Pl. XXXIV, is a diagram showing the main features of the system greatly simplified. The nephridial canal may, for convenience' sake, in description be divided into four regions; it will be understood that the transition in structure between the regions is gradual. The ventral tegumentary vessel (fig. 1, *vent. teg. v.*) sends branches over the nephridium. The small nephrostome is attached to the lower edge of the septum (figs. 1, 2, *neph. fun.*; fig. 9 *a*), which is in this region free from the ventral longitudinal muscle. Cunningham (4) was unable to ascertain definitely whether it opens into the segment in front of that containing the main body of the nephridium and the external pore; while Cosmovici (3) says, "Pour moi, chaque paire d'organes segmentaires n'est en communication qu'avec l'anneau qui la contient." Claparède, on the other hand, figured the funnel opening into the next segment (2, pl. vi, fig. 5); horizontal and sagittal sections clearly show that he was right. Frequently, however, being only suspended to the border of the septum, the nephrostome seems to swing round and open into the segment which contains the nephridium; but this is not its normal position. In its general structure it is very similar to the nephrostome of Alitta virens (4); it has, however, a nearly straight margin to its internal opening, and possesses no trace of an internal septum, as described by Cunningham in the above species. In N. diversicolor the edge or lip of the funnel is closely folded back over the outside of the organ (fig. 4, *lip of fun.*; fig. 9, *dors. lip, vent. lip*), and from this reflected surface and the margin of the internal opening (fig. 9, *int. op.*) spring long delicate processes (fig. 9, *cil. proc.*), just as in A. virens. These processes contain no nuclei, are formed of very granular protoplasm covered with long waving cilia, and must be regarded as mere outgrowths from the underlying cells. Occasionally the processes branch (fig. 3). In the nephrostome of Nereilepas fucata (fig. 9 *a*)

the lip of the funnel is not reflected, and the processes, which are longer and more delicate, spring from the margin only. The inner wall of the funnel is formed of large vesicular cells (figs. 9 and 9 *a*, *w. fun.*) with round nuclei and deeply staining inner borders; they bear numerous strong cilia (figs. 9 and 9 *a*, *int. cil.*), which beat very rapidly.

From the funnel we pass to a short, narrow, glandular region, which is not ciliated (fig. 9 *a*, *n. can.*; not shown in fig. 9), leading into the first region, the long post-septal canal (fig. 8, *p. s. can.*). The wall of this canal is composed of many glandular cells, and becomes ciliated towards the nephridial body. On entering the main compact body of the nephridium the second region of the nephridial canal becomes much convoluted, but scarcely differs in structure from the next region, except in having more nuclei round the tube, and a few cilia distributed all round the lumen.

The third region is chiefly distinguished by having a very narrow lumen, and the cilia situated only on one side of the tube (figs. 11, 16, *cil.*). The cilia may not be in a single row, but the arrangement is essentially similar to that described by Dr. Benham in Lumbricus (1); and the peculiar sinuous, wave-like effect produced by the motion of the cilia in the nephridia of most Oligochætes is visible here also.

In a transverse section of this region of the canal, one (fig. 11, *n.*) or two nuclei are generally present; I cannot say for certain whether the tube should be considered as inter- or intra-cellular. No doubt a hard and fast line of distinction cannot be drawn between the two varieties. The narrow tube which constitutes the third region of the nephridial canal is chiefly situated in the distal half of the nephridium, and leads into the fourth and last region (fig. 8).

This region is shorter and less convoluted than the last, and is situated on the under surface of the nephridium (fig. 8). Its lumen is moderately wide, and not provided with cilia (figs. 12—14); at more or less regular distances along the tube are two nuclei, situated opposite each other on either side of the lumen (figs. 12 and 15, *n.*). The nuclei in this and

other regions possess, as a rule, one large nucleolus, and sometimes some small ones in addition.

The fourth region of the nephridial canal leads directly to the exterior by means of the nephridiopore (figs. 1 and 2; fig. 10, *neph. p.*), which opens on the ventral surface of each segment, about halfway between the ventral cirrhus and the longitudinal muscles. In fig. 10 it is seen that the wall of the tube pierces the epidermis (fig. 10, *ep.*), and reaches the cuticle itself: near the pore are a pair of nuclei, one on either side of the canal.

The sections through the wall of the nephridial canal show that it is lined by a more or less definite layer (figs. 11—14, *b. l.*), which is formed of an apparently denser material than that which lies outside. This boundary layer is very well developed in the last region (fig. 14, *b. l.*). Running throughout the substance of the nephridial mass is a delicate network of some denser cuticular substance, which stains darkly with hæmatoxylin (figs. 11, 12, 12*a*, *b*, 13, 14, 16, *net.*). The boundary layer is pierced by the network, which thus reaches the lumen of the tube, and forms a close network round it. The cut ends of the threads of this network can be seen in the longitudinal section of the lumen drawn in fig. 14. Dr. Eisig describes in the Capitellids a somewhat similar though coarser mesh-work, as continuous with a boundary layer which he believes to be cuticular. In Nereis there appears to be a supporting network, and a distinct boundary layer, which is probably formed, not of cuticle, but of dense protoplasm, filled with minute granules. In some sections of a specimen preserved in Hermann's fluid (fig. 12 *a*, *ves.*) little vesicles or vacuoles can be seen piercing this layer and opening into the lumen, presumably between the meshes of the network; these vesicles probably contain some excretory products.

Fig. 12 *b* represents a small portion of the supporting network, situated between the coils of the canal, in which are seen some connective-tissue cells. These cells do not belong to the wall of the canal, and their nuclei are smaller than those of the lining cells.

The nephridium may, therefore, be described as a mass of connective tissue, in which is embedded an excretory canal, the wall of which has a small number of nuclei in it, but no distinct cell outlines.

It is well known that Ehlers (5) described the nephridium of N. cultrifera as having a long duct leading to the exterior, and a crescent-shaped internal opening. Schröder (9), who seems to have copied Ehlers' errors as carefully as his correct observations, gives a similar figure and description of the nephridium in N. diversicolor. I feel convinced that these observers, examining the nephridium after its removal from the worm, have simply mistaken the post-septal canal for the duct to the exterior, and that their internal opening is the scar left on tearing the organ away from its attachment to the body-wall at the nephridiopore. This interpretation is confirmed by the fact that Ehlers states that "die Richtung der Flimmerbewegung ging an der äusseren Mündung nach innen."

Summary and Conclusions.

We may sum up the main facts set forth above as follows:

Nereis diversicolor has in every segment, except the first and last few, a pair of large, highly differentiated, ciliated patches of cœlomic epithelium—the dorsal ciliated organs. These organs seem to occur throughout the Lycoridea, as they have been found in all the genera of that family which I have examined.

The nephridium of Nereis diversicolor consists of a compact mass, perforated by a convoluted canal, which can be distinguished into several regions, and communicating with the exterior by a short duct leading to a nephridiopore on the ventral surface. A long canal springs from the main body of the nephridium, and ends in front by a nephrostome which opens into the next segment. The nephrostome is provided with long ciliated processes. The nephridium of Nereilepas fucata is of essentially similar structure.

Reasons have been given above for considering the dorsal ciliated organ as a genital duct not fully developed. It would be premature, however, to try to come to any definite conclusion on the subject of its functions and homology until we know both its development and its fate. But I should like to point out that the Capitellidæ, the only other Polychætes possessing a nephridium described in detail which resembles that of Nereis, also have in many segments a large ciliated patch of cœlomic epithelium, which becomes funnel-shaped and functions as a genital duct (Eisig, 6). Most of the Polychæta, however, have large-funnelled nephridia which may function as carriers of the genital products. On the other hand, the latest researches on the development of the nephridia in the Polychætes (Meyer, 8) and in the Oligochætes (Vejdovsky, 10) seem to show most conclusively that these organs were developed phylogenetically from nephridia similar to those of the Planarians, which were provided with flame-cells, and did not open internally. Now Meyer has shown (8) that the large funnels in the tubicolous worms which he studied are developed independently and as outpushings of the cœlomic epithelium which join and fuse with the blind end of the nephridium. May not this funnel be the same as the genital ducts of the Capitellids and other worms (Oligochætes)? I should consider, then, that in most Polychætes the nephridium is a compound organ formed from the fusion of a tube with an outpushing of the cœlomic epithelium, as Meyer holds; and further, that in the Capitellids this funnel is partly nipped off as the genital duct, while in the Oligochætes, and perhaps in the Lycoridea also, this cœlomic funnel either has never joined the nephridium at all (most of the lower Oligochæta, Enchytræids, Naids, &c.), or that it is afterwards mostly or entirely separated off as a genital duct.

It must be remembered that if we assume that in the Chætopods the genital ducts are simply modified nephridia, and at the same time consider that their nephridia, which open into the cœlom, were derived from nephridia without internal nephrostome, but provided with flame-cells;—if we assume

this, then we must be prepared to explain what has become of the genital ducts with which the ancestors of these Chætopods were provided before their nephridia opened inwards, and why these ducts have disappeared leaving no trace behind them. On the other hand, I think that this difficulty may be avoided if we consider the original genital duct to have been a simple outpushing of the cœlomic epithelium which opened to the exterior, and afterwards became more or less grafted on to the nephridium.[1] Whether the cœlom in the Chætopods was primitively ciliated all over—as, for instance, in Rhynchobolus—is a very interesting question suggested to me by Professor Lankester. If this was the case the ciliated organs might have been formed by the restriction of the cilia to a definite area, bringing with it the specialisation of the epithelium and the development of a definite organ for a particular function.

In conclusion, I wish to express my thanks to Professor Lankester and Dr. Benham for their constant help and advice throughout my investigations.

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2. Claparède.—'Les Annélides Chétopodes du Golfe de Naples,' Suppl., 1870.
3. Cosmovici.—"Glandes génitales et organes segmentaires des Annélides Polychétes," 'Arch. de Zool. exp. et gén.,' viii, 1879–80.
4. Cunningham.—"Some Points in the Anatomy of Polychæta," 'Quart. Journ. Micr. Sci.,' xxviii, 1887.
5. Ehlers.—"Die Borstenwürmer," Leipzig, 1864–8.
6. Eisig.—'Die Capitelliden des Golfes von Neapel,' Berlin, 1887.
7. Kowalevsky.—"Ein Beitrag zur Kenntniss der Exkretionsorgane," 'Biol. Centralblatt,' ix, 1889.
8. Meyer.—"Studien über den Körperbau der Anneliden," 'Mittheil. Zool. Station Neapel," vii and viii, 1887–9.

[1] Since this was printed I have found that E. Meyer put forth very much the same theory in 1890 ("Die Abstammung der Anneliden," 'Biol. Central.,' x).

9. Schröder.—"Anatomisch-histologische Untersuchung von Nereis diversicolor, O. Fr. Müll.," 'Inaug.-Diss. Kiel,' 1886.

10. Vejdovsky.—"Entwickelungsgeschichtliche Untersuchungen," 3rd part, Prague, 1886.

EXPLANATION OF PLATES XXXIV & XXXV,

Illustrating Mr. E. S. Goodrich's paper "On a New Organ in the Lycoridea, and the Nephridium in Nereis diversicolor, O. F. Müll."

All the figures, except Fig. 9*a*, are from Nereis diversicolor, O. F. Müll.

List of Reference Letters.

ap. Aperture through the septum leading from one segment to the other. *b. l.* Boundary layer. *bl. v.* Blood-vessel. *c. b. w.* Cut body-wall. *cil.* Cilia. *cil. proc.* Ciliated processes. *circ. m.* Circular muscles. *cœl.* Cœlom. *cœl. ep.* Cœlomic epithelium. *cœl. corp.* Cœlomic corpuscles. *cut.* Cuticle. *d. z.* Dark zone. *dors. cil. org.* Dorsal ciliated organ. *dors. cœl.* Dorsal extension of the cœlom. *dors. long. m.* Dorsal longitudinal muscle. *dors. lip.* Dorsal lip of the funnel. *dors. marg. fun.* Dorsal margin of the funnel. *dors. teg. v.* Dorsal tegumentary vessel. *dors. v.* Dorsal vessel. *ep.* Epidermis. *excr.* Excretory products. *ext. cil.* External cilia. *fl. sept.* Flap of the septum. *i. limb.* Inner limb of the dorsal ciliated organ. *int.* Intestine. *int. cil.* Internal cilia. *int. op.* Internal opening. *l. mb.* Limiting membrane. *l. neph. can.* Lumen of the nephridial canal. *lip of fun.* Lip of the funnel. *lu. fun.* Lumen of the funnel. *n.* Nucleus. *n'.* Nucleus of a connective-tissue cell. *n. can.* Narrow canal. *net.* Network of supporting substance. *neph.* Nephridium. *neph. fun.* Nephridial funnel. *neph. p.* Nephridiopore. *o. limb.* Outer limb of the dorsal ciliated organ. *obl. m.* Oblique muscles. *p. s. can.* Post-septal canal. *par.* Parapodium. *sept.* Septum. *sp. m.* Sperm-morulæ. *v. marg. fun.* Ventral margin of the funnel. *vent. lip.* Ventral lip of the funnel. *vent. long. m.* Ventral longitudinal muscle. *vent. teg. v.* Ventral tegumentary vessel. *vent. v.* Ventral vessel. *ves.* Vesicles of excretory fluid. *w. fun.* Wall of the funnel. *w. neph. can.* Wall of the nephridial canal. *1st, 2nd, 3rd, 4th reg.* First, second, third, and fourth region of the nephridial canal.

Fig. 1.—Diagram of a transverse section, showing the posterior half of a segment as seen from in front. For the sake of clearness the smaller blood-vessels, setæ, and all the muscles except the four main longitudinal muscles have been omitted. The larger blood-vessels are shown on the left-hand side of the figure.

Fig. 2.—Diagrammatic side view of three segments from which the body-wall and parapodia have been removed from the left side. Only the dorsal and ventral blood-vessels are indicated.

Fig. 3.—A branching ciliated process of the nephrostome.

Fig. 4.—Portion of sagittal section through two segments—above the ventral edge of the dorsal muscle, below the dorsal edge of the ventral muscle, between the two the cœlomic cavity. The mass of fatty tissue which fills the cœlom is not represented. The anterior segment is to the right. Corrosive borax carm. Zeiss B., detail with high power.

Fig. 5.—Upper part of a slightly oblique transverse section through the middle of a segment. Corr. bor. car. Zeiss A., oc. 2, camera.

Fig. 6.—Transverse section through the edge of the dorsal ciliated organ. Corr. hæmat. Zeiss apochr. 4 mm., oc. 3, camera.

Fig. 7.—Sagittal section cutting across the dorsal extension of the cœlom. The cuticle is not represented. Corr. bor. car. Zeiss D., oc. 3, camera.

Fig. 8.—Diagrammatic sketch of the nephridium and its canal, which is subdivided into four regions.

Fig. 9.—Optical section through the nephridial funnel, drawn from the fresh, and completed from a stained specimen. Zeiss F., oc. 4.

Fig. 9*a*.—Optical section through the nephridial funnel of Nereilepas fucata, Sav., drawn from the fresh, and completed after staining with alum carmine. Zeiss apochr. 4 mm., oc. 4, camera.

Fig. 10.—Portion of a transverse section, showing the nephridiopore. Corr. bor. car. Zeiss apochr. 4 mm., oc. 8, camera.

Fig. 11.—Transverse section through the third region of the nephridial canal. Corr. hæmat. Zeiss 2 mm. oil im., oc. 8.

Fig. 12.—Transverse section through the fourth region of the nephridial canal. Corr. hæmat. Zeiss apochr. 4 mm., oc. 8.

Fig. 12*a*.—Transverse section through the third region of the nephridial canal. Hermann, hæmat. Zeiss 2 mm. oil im., comp. oc. 4.

Fig. 12*b*.—Section through the tissue between the coils of the nephridium, showing network and connective-tissue cells. Hermann, hæmat. Zeiss 2 mm. oil im., comp. oc. 4.

Fig. 13.—Transverse section, slightly oblique, through the fourth region of the nephridial canal. Corr. hæmat. Zeiss 2 mm. oil im., oc. 8.

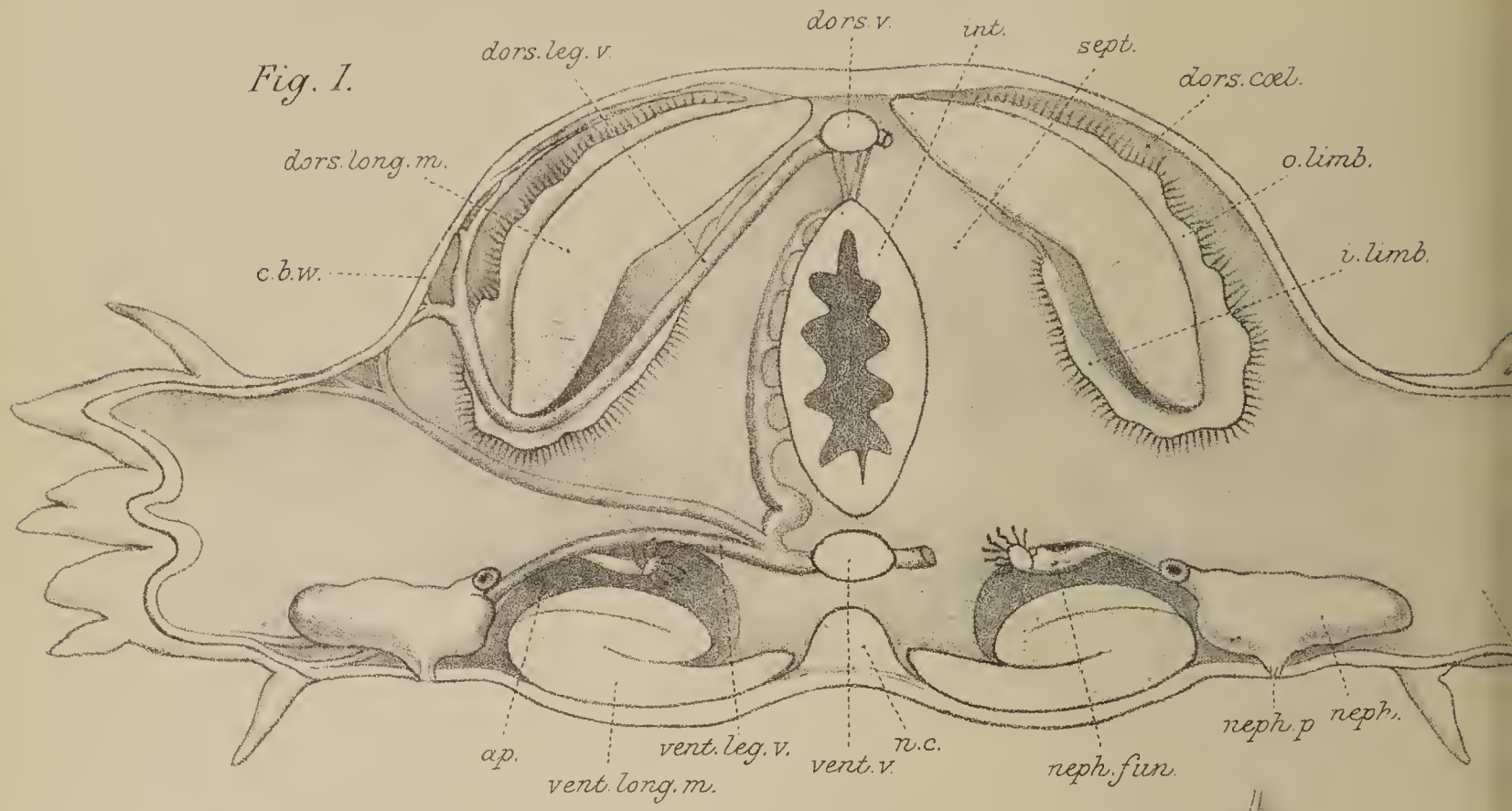
Fig. 14.—Section through the fourth region of the nephridial canal. The lumen not being straight, the wall of the canal is cut through here and there. Corr. hæmat. Zeiss apochr. 4 mm., oc. 4, camera.

Fig. 15.—Portion of a transverse section, showing the dorsal muscle and dorsal ciliated organ cut through. Corr. hæmat. Zeiss B., oc. 4, camera.

Fig. 16.—Longitudinal section through a piece of the third region of the nephridial canal. Corr. hæmat. Zeiss apochr. 4 mm., oc. 4, camera.

Fig. 17.—Portion of a horizontal section, about midway through the intestine. Corr. bor. car. Zeiss A., oc. 3, camera.

Fig. 1.



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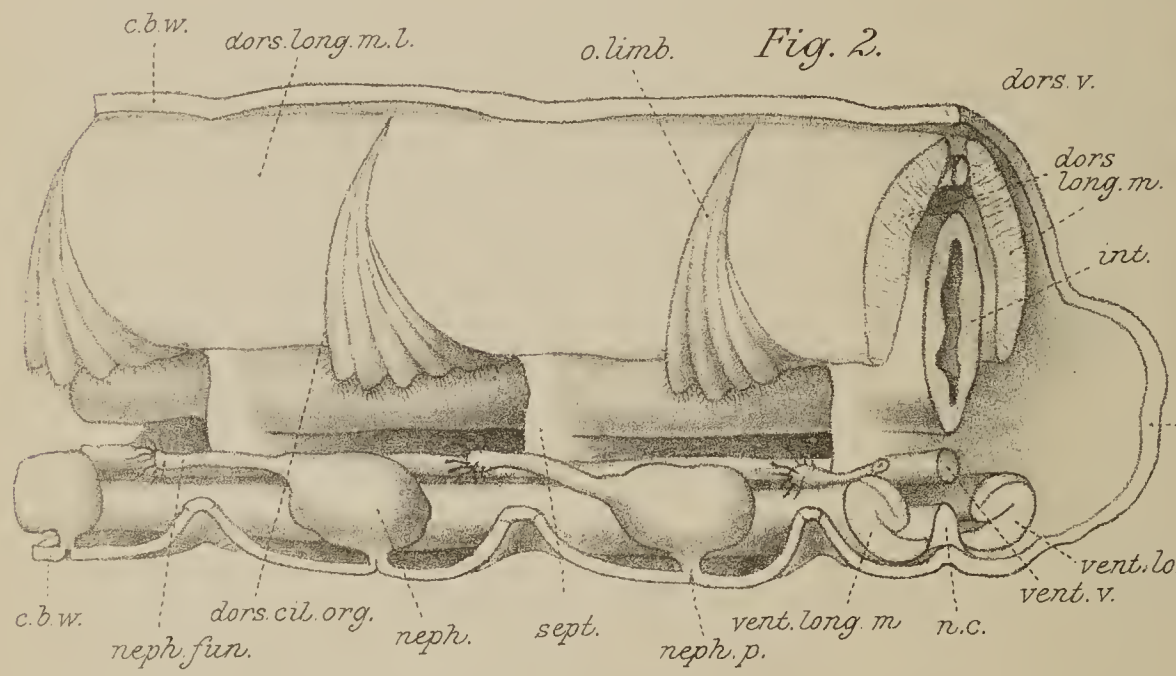

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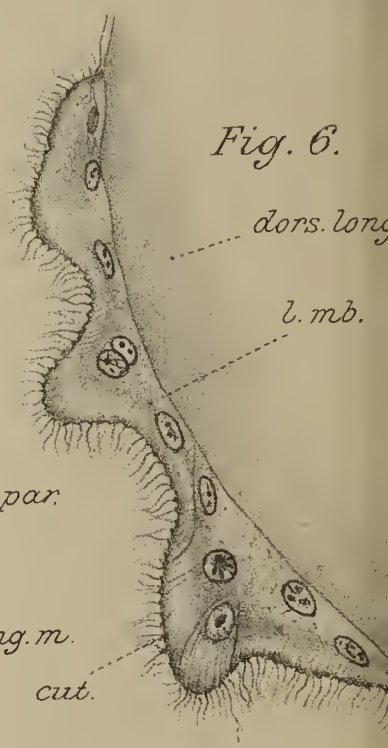

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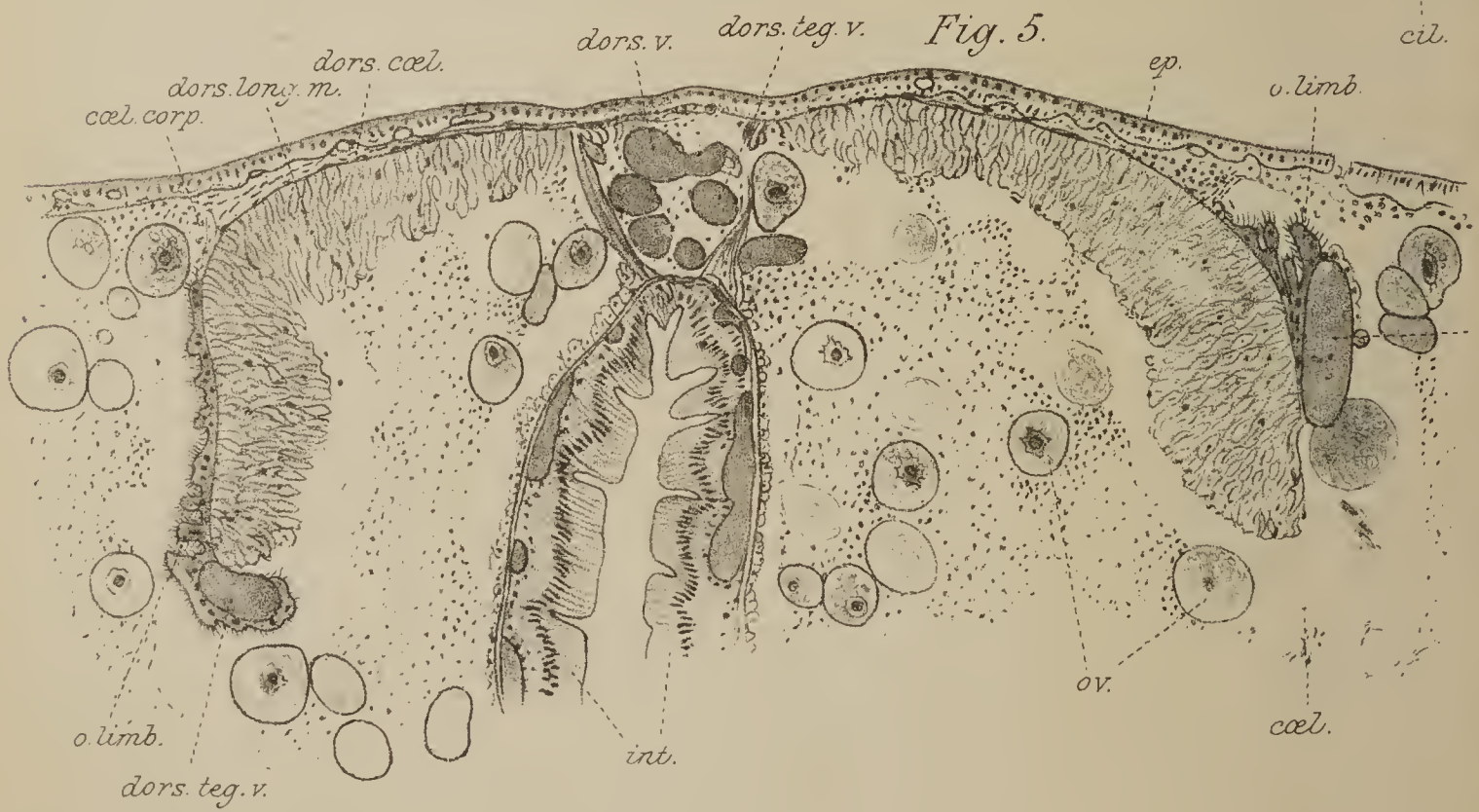

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Fig. 4.

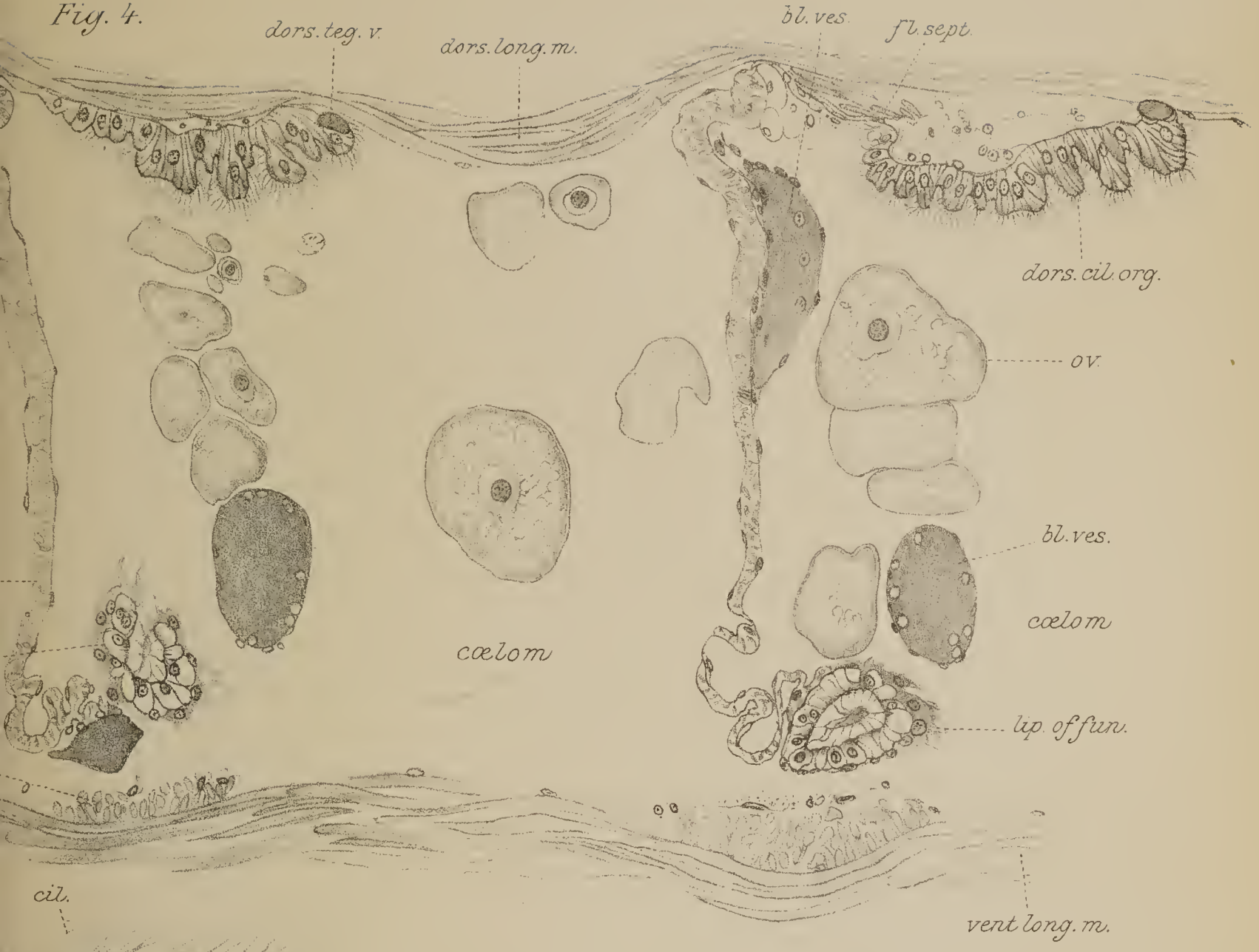

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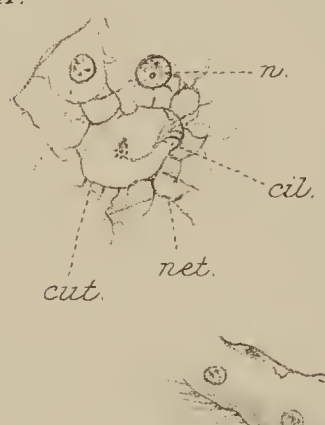
Fig. 9 a

Fig. II.



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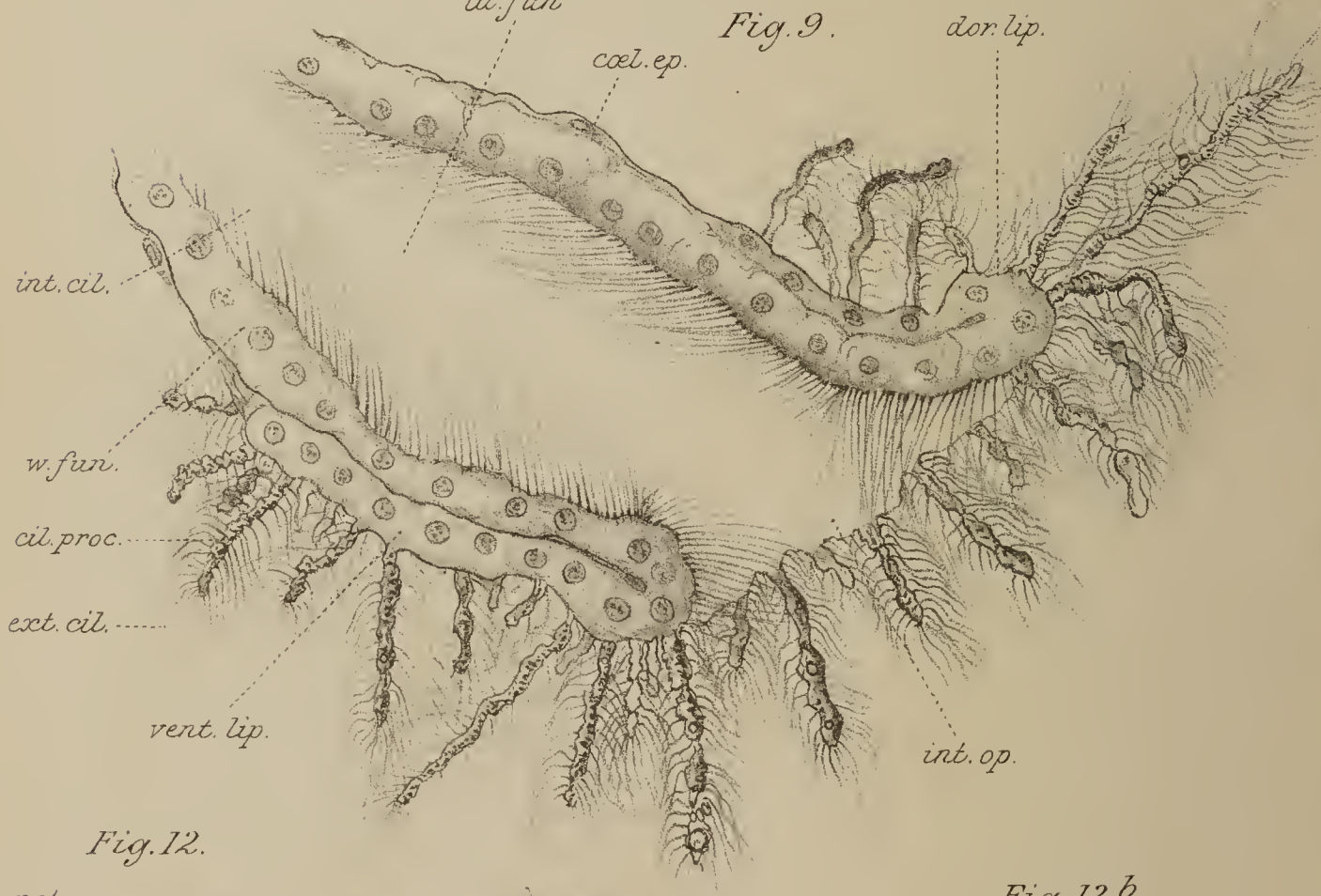

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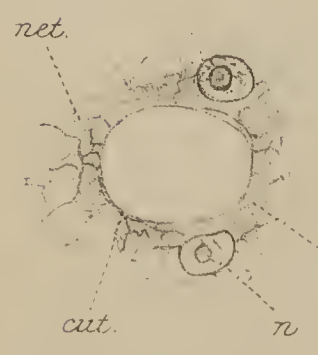
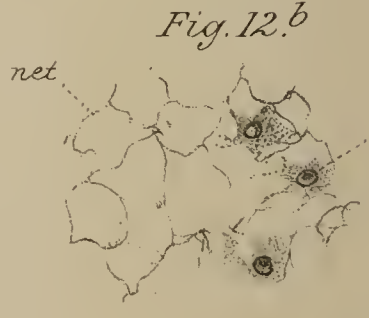


Fig. 12 a

Fig. 12. b



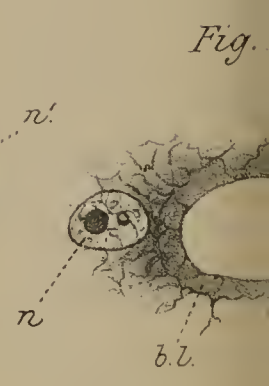


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Fig. 10.

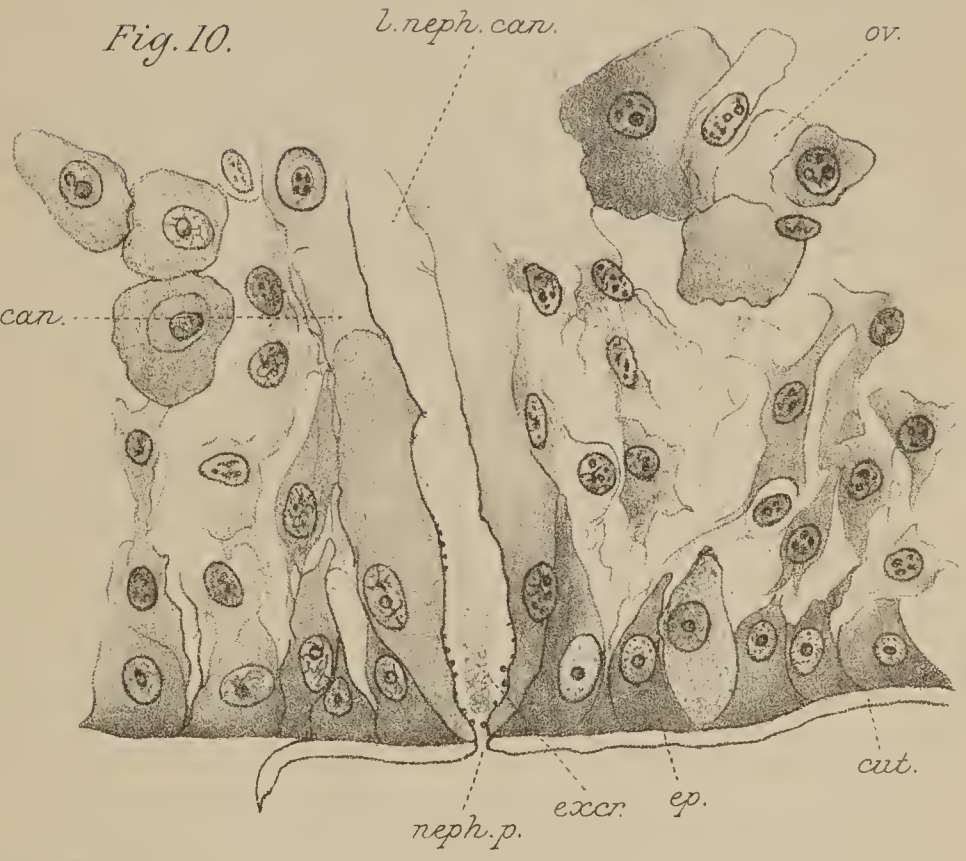


Fig. 16.

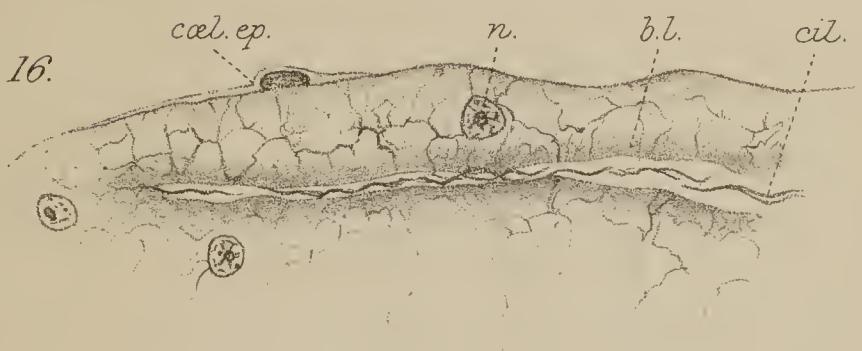
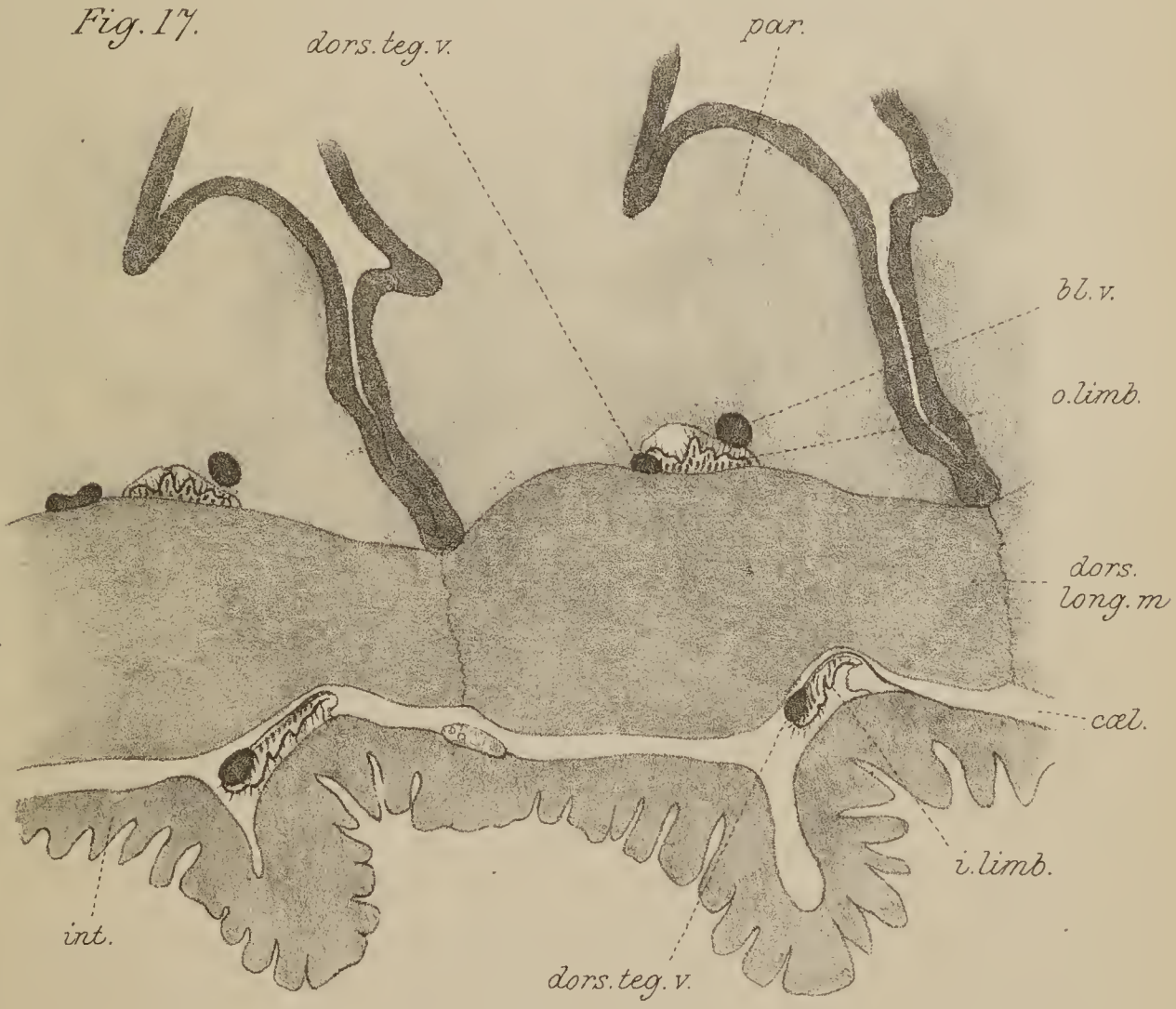


Fig. 17.



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Note on the Cœlom and Vascular System of Mollusca and Arthropoda.

By

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The reference by Mr. Allen in his memoir published in this number of the Journal to a note by me appended to Dr. Gulland's paper in 1885 on "The Coxal Gland of Limulus" induces me to reprint here the report of a paper which I read to Section D at the Manchester meeting of the British Association in 1887. This report was furnished by me to 'Nature,' and printed in that journal in March, 1888 (p. 498). Professor Julin, of Liège, also published—in a report made by him to the Belgian Academy on the proceedings at Manchester—an abstract of the same paper. The report printed in 'Nature' is as follows:

"The object of the author was to establish the fact that the system of blood-containing spaces pervading the body in Mollusca and in Arthropoda was not, as sometimes (and indeed usually) supposed, equivalent to the cœlom or perivisceral space of such animals as the Chætopoda and the Vertebrata, but was in reality a distended and irregularly swollen vascular system—the equivalent of the blood-vascular system of Chætopoda and Vertebrata. Hence he proposed to call the body-spaces of Mollusca and Arthropoda 'hæmocœl,' in contradistinction to 'cœlom.' It had been held by previous investigators that in Mollusca and Arthropoda the cœlom and the vascular system were united into one set of spaces—whether by a process of gradual fusion, or owing to the fact that the two systems had never been differentiated from a common

original space representing them both in the ancestors of these two great phyla. The author stated that he had been led to the view which he now formulated by his discovery of distinct spaces in both Mollusca and Arthropoda, which appear to be the true cœlom, and are separate from the swollen vascular system.

"In Mollusca the pericardial space is the chief representative of cœlom. It is usually taught that the pericardium of Molluscs contains blood, and is in free communication with veins; but the author had succeeded in showing by observations on the red-blooded Solen legumen (already published, 'Zoolog. Anzeiger,' No. 170, 1884), and by more recent careful investigation of Anodonta cygnea, Patella vulgata, and Helix aspersa, that the pericardium has no communication with the vascular system, and does not contain blood. The perigonadial spaces (so-called generative glands) and the pericardial space (which has arborescent tubular outgrowths in some Lamellibranchs forming Keber's organ) are, then, the cœlom of the Mollusca. It is quite distinct from the hæmocœl. In Cephalopods, and in the archaic Gastropod Neomenia, the pericardial and perigonadial cœlomic remnants are continuous, and form one cavity. There is strong reason to believe that in ancestral Molluscs the hæmocœl was more completely tubular and truly vasiform than it is in living Molluscs. In the later Molluscs the walls of the vessels have swollen out in many regions (especially the veins), and have obliterated the cœlom, which has shrunk to the small dimensions of pericardium and perigonadium. There are, however, many Molluscs with complete capillaries, arteries, and veins, in certain regions of the body. These had been recently studied by the author by means of injections, and by silver impregnation, and drawings illustrative of them were exhibited to the Section.

"With regard to the Arthropoda, Professor Lankester formulated the same view, viz. that the ancestral blood-vessels have swollen and enlarged, especially the veins, so as to form large irregular spaces, which have blocked up and so obliterated the

previously existing cœlom. Nevertheless the cœlom still persists in some parts of the Arthropod body quite separate from the swollen blood-vascular system. It persists as the tubular generative glands (perigonadium), and also as a system of small spaces (lymph-system) in the connective tissue of Astacus and of Limulus, and as the internal terminal vesicle of the green glands and other nephridia present in various Arthropoda. Professor Lankester stated that he had been led to this view with regard to the vascular system and cœlom of the Arthropoda by the results of his histological investigations on the vascular system and connective tissues of Astacus and Limulus, and by the results obtained in his laboratory by Mr. Gulland in studying the development of the nephridial 'coxal gland' of Limulus (already published, with note by Professor Lankester, in the 'Quart. Journ. Micr. Sci.,' 1885, vol. xxv, p. 515). He had also been led to this view by the attempt to explain theoretically the origin of the peculiar structure of the Arthropod's heart and blood-holding pericardium.

"The Arthropod's heart and pericardium are absolutely peculiar to the group, and characteristic of all its members, even of Peripatus. The author had asked himself how the existence of a tubular heart with paired valvular apertures in each segment of the body, lying within a blood-holding sac, could be explained. He conceived that it might best be explained by that tendency of the veins to dilate and to form irregular large blood-sinuses, which on other grounds we have reason to consider as a structural tendency of Arthropods. Each pair of valvular apertures in the Arthropod's heart represents a pair of distinct tubular veins, which in the ancestors of the Arthropoda brought blood to the heart from the gills. These veins have dilated, and their adjacent walls have been absorbed, so that we now have, instead of a series of veins, a great continuous blood-sinus on each side of the heart or dorsal vessel.

"Capillaries of the finest dimensions were shown by Professor Lankester to exist in certain parts of Astacus and of Limulus. In studying these he had come across the remnants of cœlom.

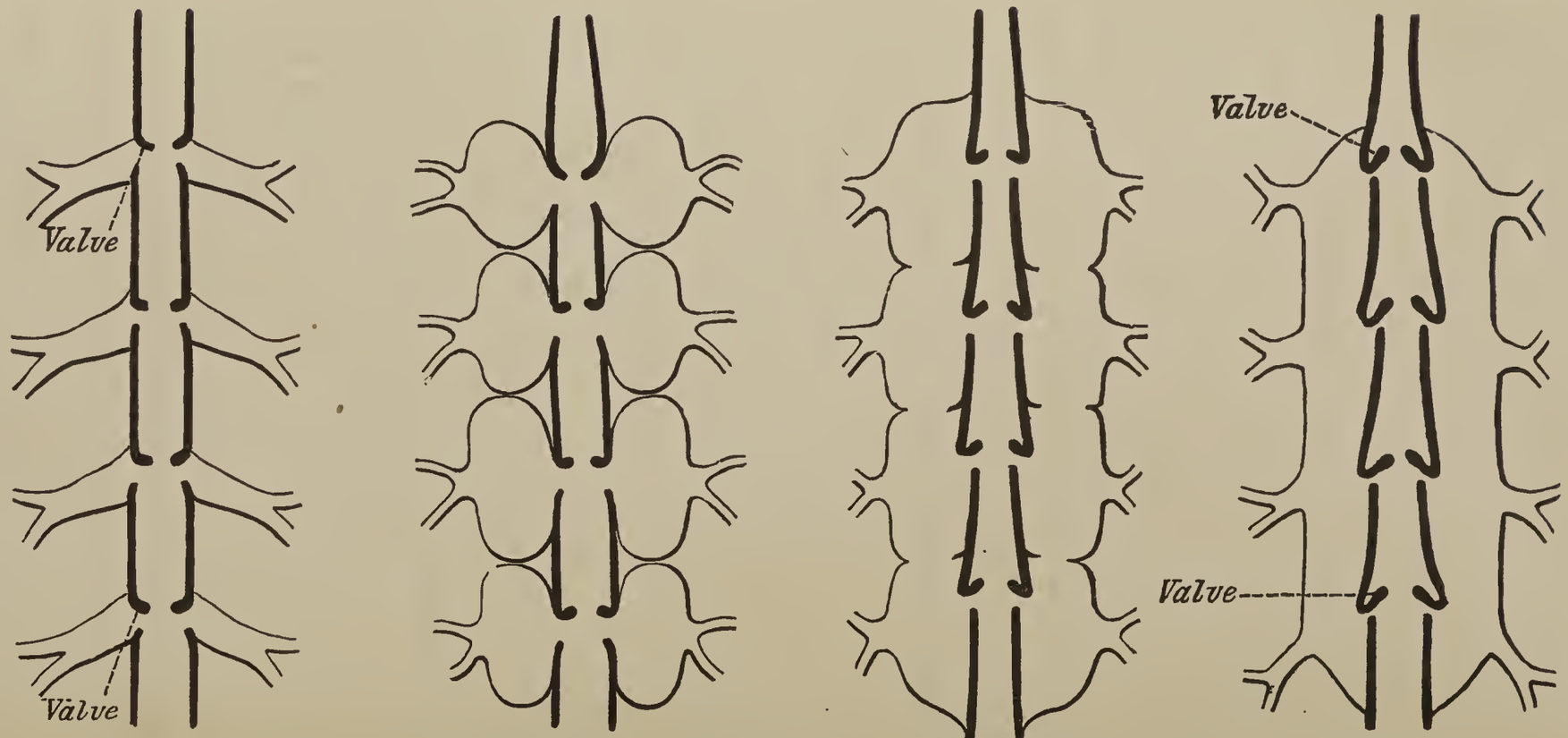

Fig. A. Fig. B. Fig. C. Fig. D.

DIAGRAMS ILLUSTRATING PROFESSOR LANKESTER'S THEORY OF THE DEVELOPMENT OF THE ARTHROPOD HEART AND PERICARDIAL SINUS.

Fig. A.—Dorsal vessel and veins with valves at their junction with the dorsal vessel. Chætopod stage.

Fig. B.—Hypothetical. The veins dilated.

Fig. C.—Hypothetical. The veins further dilated and now made confluent by the absorption of their adjacent walls.

Fig. D.—Arthropod heart with four pairs of ostia and a pericardial blood-sinus.

Between the capillaries and unconnected with them—in the connective tissue of both Astacus and Limulus—is a system of spaces containing a coagulable fluid. (These spaces were described and figured in Limulus in 1884 by Professor Lankester in the 'Quart. Journ. Micr. Sci.') It is into this system of spaces that the tubular nephridium which becomes the coxal gland of Limulus opens. Hence these spaces are remnants of the cœlom, elsewhere blocked up and obliterated by the swollen veins which form the hæmocœl. The tubular generative glands of Arthropods are to be explained as perigonadial cœlom communicating with the exterior through modified nephridia. Beddard's discovery of such a condition of the ovary and oviduct in the earthworm Eudrilus is confirmatory of this explanation.

"The views which had been thus arrived at by Professor Lankester, and very briefly indicated in the note in the 'Quart. Journ. Micr. Sci.,' 1885, p. 515, have received a startling and demonstrative confirmation in Sedgwick's brilliant results as to the development of cœlom and hæmocœl in Peripatus, published in the 'Quart. Journ. Micr. Sci.,' February, 1888, and announced early in 1887 to the Cambridge Philosophical Society."

To this brief statement I may now add that it has been for some time my desire to obtain well-preserved specimens of Lernanthropus, the remarkable Copepod with a tubular vascular system containing hæmoglobinised blood, first described as possessing this peculiarity by Edouard van Beneden, and subsequently figured and described in detail by Heider ('Arbeiten Zool. Inst. Wien,' Bd. ii, 1879). It would be extremely important to ascertain, if possible, whether the tubular vascular system of Lernanthropus co-exists with spaces which can be identified with the supposed hæmocœl of other Crustacea, or whether, as should be the case if my theory is correct, the spaces in Lernanthropus, which are not in continuity with the red vascular system, can be identified as "cœlom," and distinguished from "hæmocœl spaces."

I have failed to obtain Lernanthropus either from Plymouth

or from Naples. If any naturalist reading these lines should be able and willing to furnish me with specimens he would confer a great favour on me by communicating with me.

The question in regard to Lernanthropus may be further stated in this way: is the tubular vascular system of that animal an heirloom from Annelid-like ancestors with the characteristic Chætopod's vascular system? or is it a special development de novo peculiar to this Copepod?

One of the most attractive features about the theory of dilated veins in the Arthropods is the simple explanation which it affords of an otherwise puzzling structure, namely, the Arthropod heart. I therefore venture to present here a diagram which I have made use of during the last six years in my lectures illustrating the possible—I think we may say the probable—steps by which the Arthropod heart, with its curious valvate ostia and blood-holding pericardial space, was developed from the dorsal vessel of a closed "tubular" vascular system such as that of the earthworm.

The Structure of the Pharyngeal Bars of Amphioxus.

By

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With Plates 6 and 7.

It may be thought that the structure of the pharyngeal bars of Amphioxus is sufficiently known, after the description by Lankester, and more recently by Spengel; but there still remains a certain amount of doubt as to some points in the structure of the tongue or secondary bar, although recent authors are in agreement as to the general structure of the primary bar. It is to the tongue bar, therefore, that I have more particularly directed my attention.

Spengel contradicted Professor Lankester on several points, both with regard to matters of observation, and more especially with regard to certain interpretations, in a very dogmatic and, indeed, discourteous manner. I was surprised to find that Professor Spengel himself is by no means correct in sundry matters of mere observation.

It will be remembered that Lankester, in addition to his account of the structure of the gill bars—which was, like his figures, in great advance of the work of previous writers on the subject—made certain statements with regard to the spaces within these bars; he attempted to distinguish, not only in the

bars, but in Amphioxus as a whole, cœlomic spaces from blood-vessels. It is chiefly with regard to the interpretation of the spaces within the tongue bars that Spengel joins issue with him, and it was to this part of the subject that I directed my attention last summer in the endeavour more especially to decide whether the cavity traversing the "chitinoid" rod of the tongue bar be cœlom (Lankester) or blood-vessel (Spengel).

I hoped to decide the question by the examination of specimens which had been fed with carmine; and for this purpose Professor Lankester requested Mr. A. Willey, who was then at Naples, to feed some animals and preserve them for me. My thanks are due to Mr. Willey for so doing. Unfortunately, however, these carmine-fed specimens have not been of much value for my purpose, and I was compelled to fall back upon carefully preserved specimens (in picro-sulphuric acid) stained in various media. This was the method followed both by Lankester and by Spengel—careful tracing of spaces from section to section in order to ascertain their communication with other cavities about whose nature there is no doubt.

Before I had completed my work, Boveri's most interesting paper on the nephridia was published. Boveri found, as I had, that Spengel, both in incomplete observation and in certain interpretations, had fallen into errors similar to those which with an accompaniment of gratuitous insolence he had attributed to Lankester.

This short note may conveniently be divided as follows:

A. Description of the tongue bar, according to my own observations, and comparison of it with the primary bar.

B. Interpretations of the parts of the tongue bar.

C. The observations of recent observers.

D. Certain abnormalities in the pharyngeal bars.

The authors who have described and figured the gill bars of Amphioxus, to whom I shall have occasion to refer, are—

1. Stieda.—"Studien üb. d. Amphioxus lanceolatus," 'Mém. Ac. Sci. Pétersbourg,' xix, 1873.

2. Langerhans.—"Zur Anat. d. Amphioxus lanceolatus," 'Arch. f. mikr. Anat.,' xii, 1876.
3. Schneider.—'Beiträge zur Vergleich. Anat. und Entwickel. der Wirbelthiere,' 1879.
4. Lankester.—"Contributions to the Knowledge of Amphioxus lanceolatus," 'Quart. Journ. Micr. Sci.,' xxix.
5. Spengel.—"Beit. z. Kenntniss d. Kiemen des Amphioxus," 'Zool. Jahrbuch' (Anat.), iv, 1891.
6. Boveri.—"Die Nierencanalchen des Amphioxus," 'Zool. Jahrbuch' (Anat.), v, 1892.

In addition to these, a bibliography relating to Amphioxus will be found in Lankester's paper.

A. The Tongue Bar.

The tongue (or secondary) bar is usually distinguished from the primary bar (*a*) in being supported by atubular skeletal rod in place of the double rod of the primary bar, (*b*) and in being without any cœlom between the rod and the atrial epithelium. It is unnecessary to describe the relations of the bars to one another or to neighbouring parts of the animal, as these matters have been fully described and illustrated by recent writers on the subject.

The structure of the bar is most readily seen in its transverse sections, but such sections—accurately transverse to the bar—are not so easily obtained; in sections transverse to the long axis of Amphioxus, only one or two bars on each side of the pharynx will be cut transversely, though in the pre-hepatic region more bars are so cut, and still more are very nearly transversely cut, than is the case posteriorly. But by varying the obliquity of the plane of section to that of the long axis of the body, I was able, ultimately, to obtain sections which cut nearly the whole series of bars in any section almost accurately at right angles to their length.

It appears to me that this is most important, for the discrepancies in various descriptions and figures of the bar are doubtless due to the more or less obliquity of the sections.

Another matter which must be taken into serious account is the mode of preparation and the character of the stain; for I

have noted in my series—treated differently in both these respects—various differences due to shrinkage and such effects, which suggest the cause of certain omissions by some authors, and of wrong interpretations and other errors.

I have found that Kleinenberg's fluid (picro-sulphuric acid) is the preservative which produces less distortion than other reagents. Cochineal stains, especially Mayer's alcoholic cochineal, serves best for the demonstration of blood in the vessels and for the examination of the skeletal tissues.

Hæmatoxylin is, of course, useful for the nuclei, but cochineal gives better results in the case of cell-bodies.

Some of the animals were stained in bulk; in other cases the sections were stained on the slide.

I proceed now to a description of a transverse section of a tongue bar, as elucidated by the examination of sections treated in different ways, as well as of isolated portions of pharyngeal wall.

Such a section is a narrow bar (about three times as long as it is wide), presenting two ends and two sides: one end, the Outer end, projects into the atrium, and is covered by atrial epithelium; the opposite end, or Inner end, projects into the cavity of the pharynx, and is lined by hypoblast. The sides are directed (roughly) anteriorly and posteriorly.

The bar consists almost entirely of columnar epithelial cells, the inner ends of which abut upon a membrane, the cutis (I follow here Professor Lankester), throughout the greater part of the bar; whilst at the outer end the cells rest upon the skeletal rod, which I regard as merely a specialised part of this cutis.

The character of the epithelium, however, differs at the two ends and at the sides. At the Inner or pharyngeal end the nuclei are arranged in three groups, a central group and a lateral group on each side, as Lankester was the first to point out. The nuclei of the central group are arranged in two more or less curved rows (as in fig. 1), but this arrangement is due not to the existence of two layers of cells, but to the fact that alternately the nuclei are situated nearer to or

further from the base of the cell. The nuclei are elongated and oval; they are placed much closer to one another than my figure represents, and as they stain deeply are very conspicuous. In thick sections it is difficult to determine whether one has to do with a single row of very elongated cells (as Lankester believed), or with several rows of them; this difficulty is emphasised when the sections are not accurately transverse. But in thin sections, successfully cut, it is easily seen that the nuclei are arranged as I describe them.

The cells to which these nuclei belong are, therefore, as long as the epithelium is thick; they are very narrow peripherally and swollen at the nuclear level, producing the flask-shaped appearance of the whole group. These cells carry cilia which are considerably longer than those carried by the lateral groups of cells at this inner end; and it is curious that of previous observers, only Spengel and Boveri have noted this special bundle of cilia. The free ends of the cells are provided with a very finely striated border, which comes out well in cochineal preparations, but which is not differentiated by other stains used.

Each lateral group of nuclei consists of a single row curving downwards from the central group towards each side, somewhat in the way represented by Lankester; but I find that these nuclei, which are long and narrow, are not arranged quite in the fan-shaped manner represented by him.

The cells containing these nuclei carry quite short cilia—entirely overlooked by Spengel and Boveri,—and their free ends are not provided with a striated border. The shape of this inner end has been very variously represented, as the copies of previous figures on Pl. 6 will show.

The side of the bar presents some four or five rows of small nuclei forming a broad band, about two thirds the whole width of the epithelium. These nuclei are not circular, as most observers have represented them (owing to the obliquity of the section, as I know from experience), but are oval, with the long axis directed vertically to the plane of the surface. Langerhans appears to have noted their oval shape.

Here, again, these rows of nuclei do not represent as many layers of cells, for there is but a single layer of very long and very narrow cells, with the nuclei at different levels in neighbouring cells. In some of my preparations these cells are more or less macerated, so that I was able to confirm the description of them given by Langerhans (see fig. 19). Each cell, or at any rate most cells—for it is impossible to be absolutely certain that all the cells reach the surface, though I believe this to be the case—carries a single very long cilium, and presents a finely striated border. The nuclei of the lowermost row appear to be slightly longer than those of other rows, and are close to the septal membrane or cutis, along which they form a very well-marked series. Towards the extremity of the side, both outwards and inwards, i. e. towards the atrial end and the pharyngeal end, the lowest row of nuclei curve upwards towards the surface, so that the epithelial cells become shorter and shorter, and the number of rows less and less, till finally there is but a single nucleus contained in a cell not much longer than itself (see fig. 1). At the inner end of the bar the thin membrane-like cutis curves outwards towards the surface, and naturally the row of nuclei take on this curvature. At the opposite end of the bar the row of nuclei follow the curve of the chitinoid rod; but at this end, for a short space, the epithelium is overlapped, as it were, by a row of three or four cubical cells containing pigment, and not carrying cilia. These cells are part of the atrial epithelium, the invaginated epiblast of the pharyngeal slits. These pigmented cells differ from those hitherto mentioned in containing circular (spherical) nuclei, and herein agree with the cells constituting the epithelium of the Outer end of the bar.

This atrial epithelium is characterised by the larger size of its cells, the absence of cilia, and the presence of relatively small round nuclei, which are placed at different levels in the cells (fig. 1). These cells are highest in the middle of this end —i. e. at the end of the long axis of the section through the bar —and decrease in length at each side of this point till they graduate into the cubical pigmented cells which overlap the

cells of the sides of the bar. In the tongue bar these cells are all of one kind (fig. 18), whereas in the primary bar two kinds of cell (fig. 17, *a*, *b*) are present, one (*a*) being vacuolated, the other (*b*) more granular. Langerhans noted this fact, though he exaggerated the difference. So much for the epithelium of the bar. I shall point out later how far these statements of fact differ from those of my predecessors.[1]

Turning now to the cutis of the bar, i.e. the septal membrane and the chitinoid rod: the septal membrane forms a very thin sheet of tissue traversing the greater part of the long axis of the section, and separating the epithelium of the two sides. At the base of the epithelium of the Inner or pharyngeal end of the bar the septal membrane splits into two, and each of the two branches curves outwards towards the surface; this forking of the membrane leaves a V-shaped space, which is converted into a triangle by a membrane (cutis) at the base of the pharyngeal epithelium.

In this triangular space is a blood-vessel, as Spengel and Boveri have already described (figs. 7, 8). It may be called the internal or Visceral vessel. At the opposite end the septal membrane similarly divides into two, each half of which appears to be continuous with the corresponding side of the rod (fig. 1). This space, which differs somewhat in shape according to the shape of the rod, but which is, on the whole, triangular, also contains a blood-vessel—the external, or somatic vessel. This vessel was observed by Lankester (fig. 6), but overlooked by Spengel (fig. 7), although he represents the space here, whilst Boveri described it as existing only in the primary bar. From the fact that, at each extremity, this septal membrane forks, and from theoretical considerations, I believed this membrane to be in reality double, as indeed it is represented by Stieda's figure (Pl. 6, fig. 3). But I was for a long time unable to assure myself of this fact. I was unable to satisfy myself as to the presence of two membranes here, for, owing to the refrangibility of the structure, it is difficult to make certain whether

[1] I have not observed the "muscle-cells" in the bar described by Rohon and by Langerhans, J. Müller and Schneider.

one sees a double outline to the single membrane (such as Boveri represents, Pl. 6, fig. 8) or two closely apposed membranes.

Spengel vehemently animadverts on Lankester's interpretation of this membrane as a mesoblastic cutis, and insists on its being a "basement membrane," i.e. epiblastic. Lankester was, it seems to me, in error in referring the origin of this membrane to the deepest layer of nuclei in the sides of the bar; at the same time, if we consider the relations of this membrane to the rod and to the vessels at each end, we cannot doubt that the rod and the membrane have the same origin. The rod would scarcely, I presume, be referred by Spengel to the epiblast. I believe, however, that I have decided that the rod is mesoblastic by the discovery of the flattened nuclei pressed against its inner surface (Pl. 7, fig. 13); and we may conclude that the rods in both bars are produced by the flattened epithelium which, as Hatschek has pointed out, forms the "connective tissue" throughout the body of Amphioxus. If the rod is mesoblastic, then a priori we may believe the eptal membrane, which is absolutely continuous with it, to be also mesoblastic; but further, I have detected flattened nuclei in this axis of the bar, i.e. between the two halves of the closely apposed membranes. I searched long and carefully for any nuclei in relation to the septal membrane, and ultimately, in my series of accurately transverse sections, I was able, with the aid of Zeiss's apochromatic, to observe some structures which I believed to be nuclei. However, I was not absolutely certain of their existence, owing to the refrangibility of the membrane and the denseness with which the epithelial nuclei are packed; but in a series of sections intended to be horizontal, and stained in hæmatoxylin, some of the bars were cut longitudinally for a considerable distance—some six or seven times the length of an ordinary transverse section of a bar,—and here I saw distinctly elongated and much compressed nuclei (fig. 21) of fair size, lying between the two membranes. These, like the nuclei surrounding cœlomic spaces, are not rich in chromatin, and do not take the stain easily. We may,

therefore, conclude—as, from a priori reasoning, we should be led to believe—that this septal membrane is double, and is mesoblastic, and not a basement membrane.

The chitinoid rod of the tongue bar is distinguished, as is well known, from that in the primary bar by the presence of a canal—it is a perforated rod.

The shape of the section of the rod varies considerably, both in different bars and even in different parts of the same bar, but that represented in this figure may be regarded as the most general shape. Not only the general outline, but the shape and extent of the contained space are included in the above statement as to the variability of the rod. Professor Lankester has already figured several such variations (loc. cit., pl. xxxvi, B), and others will be found on the plate illustrating this note (Pl. 7, figs. 13—16). But most generally the rod presents a somewhat triangular section, with rounded angle at the base, and a notch—more or less profound—at the apex. This notch forms a part of the internal triangular cavity partially bounded by the septal membrane and occupied by the somatic blood-vessel.

The chief cavity—the canal—of the rod is similarly more or less triangular in section, rarely round, as Lankester represents it, though this shape does occur. The thickness of the outer wall presents very interesting variations: more usually it is nearly as thick as the sides, but it may be very much thinner (as in fig. 14); it may be represented merely by a thin membrane little thicker than the septal membrane, and much thinner than the cutis (basement membrane—Spengel) below the atrial epithelium of the primary bar. Further, this rod may be represented by a couple of curved pieces, which do not quite meet externally, so that the curtained cavity is without an outer wall (fig. 15). This is always the case at the points where a synapticulum joins the tongue bar (fig. 31), but it also occasionally occurs elsewhere.

This cavity frequently appears quite empty, invariably so in my hæmatoxylin preparations; but in sections stained with cochineal, granular matter is very frequently present in greater

or less abundance;[1] and I have sometimes noticed an apparent division of this cavity by a transverse partition, the granulations having a slightly different appearance in the two sides of this partition (fig. 14). Moreover in this same series of sections, as also in sections stained with Weigert's picrocarmine, the blood in undoubted blood-vessels, such as hepatic vessels, dorsal and subendostylar vessels, takes on a characteristic deep red colour—deeper than the tint taken by the skeletal tissues,—so that I am able most definitely to state that there are three blood-vessels traversing the tongue bar, not two, only as Spengel and Boveri believed (c.f. fig. 1 with figs. 7, 8).

Of these three vessels, two occur always at opposite extremities of the septal membrane, in the triangular spaces already mentioned; the third lies inside the rod, and may be called the skeletal vessel. Usually it has the position represented in fig. 1—in the chief canal of the rod, but it does not appear to fill this canal; I can generally detect a slight space around it. This may, of course, be due to shrinkage of the clotted blood; but the apparent existence in some cases of a partition (see fig. 14 and the explanation of it) favours my view, as also does the condition of things represented in fig. 13, where the vessel is passing out of the cavity, that this cavity of the rod is cœlom, which contains a blood-vessel. This view is further strengthened by the fact that, both in my hæmatoxylin preparations (where the blood-vessels are not evident) and in my cochineal sections, I have detected flattened nuclei pressed against the inner surface of the rod, as represented diagrammatically in fig. 1, and accurately drawn from the object in fig. 13. This, I may say, has not been an occasional occurrence, but can be seen in many accurately transverse sections of the bar.

In some of the variations from the normal the rod presents a small cavity about midway between the main canal and the apical notch (figs. 13, 14), and this cavity is usually connected

[1] Spengel mentions the presence of finely granular material in the canal of the hollow rod (loc. cit., p. 278).

with the former by a narrow channel; in this accessory cavity I have sometimes seen a vessel in addition to that in the chief canal, and sometimes I have not detected the latter. I take it that there may be occasional anastomosis between the "somatic" vessel in the notch and the skeletal vessel in the canal.

Comparison of the Tongue Bar and Primary Bar.

I wish now to compare such a transverse section of a tongue bar with that of a primary bar, so far as regards the Outer end. Compare my figures 1 and 2 and that copied from Boveri (fig. 12). In the primary bar Boveri describes, as I myself find, three vessels—(*a*) the inner, or visceral, and (*b*) outer, or somatic, as is the case in the tongue bar, and (*c*) the third or skeletal (first observed by Spengel) outside the cœlom of the primary bar, between the atrial epiblast and the "cutis" (basement membrane of Spengel). This last vessel may project through the cutis into the cœlom, and at the base of the bar, where it springs from the endostyle, and where the rod forks, this blood-vessel lies in the angle of the fork, i. e. in the cœlom itself (fig. 30, *a*), as Spengel has figured. In the tongue bar the first two of these vessels are identical with those of the primary, and one can scarcely resist the idea that the third, or skeletal vessel inside the rod, may correspond with the subepidermal vessel of the primary bar; it differs from it, however, in one very important point, namely, in the absence of any connection with the subendostylar vessel. But now turn to the rod itself. This is, in the primary bar, made up of two pieces, more or less fused according to the region of the bar (see fig. 30, *a*, *b*, *c*), so as to form a triangle, usually with a more or less pronounced notch, or linear channel, arising from near the base (see fig. 9); or again, as Schneider figured and as I have frequently observed, a triradiate split in its centre[1] (fig. 30, *c*). Outside the rod comes the cœlom—every one is agreed about that—lined by flattened cells; and outside them the cutis,

[1] This usually is due to the softer nature of the central part of this rod, and is not really a cavity: the rod presents irregularly concentric markings, as if shrunk, and is firmer externally.

which varies considerably in thickness, and can be traced, as Boveri's figure shows, into the rod at each extremity (Pl. 6, fig. 12). This cutis stains exactly like the rod in cochineal, and also like the rod is unstained in hæmatoxylin. Sometimes the cleft in the rod is more pronounced, and gives rise to a more definite channel (see Lankester, xxxvi B, fig. 3, *f*) open to the cœlom. Such a condition of things is represented in my Pl. 7, fig. 31, which passes through a primary rod (P. 1) at the level of a synapticulum,[1] and should be compared with certain variations in the rod of the tongue bar in the same figure and in fig. 15, and one is struck with the resemblance between the two.

I would suggest that the distinction between the two rods, viz. that of the primary bar and that of the tongue bar, is not so profound as one would be led to think from the use of the terms solid (or bifid) rod and hollow rod. We have seen that not infrequently the rod of the tongue bar is formed of two pieces (fig. 15), whilst, on the other hand, the rod of the primary bar may enclose a cavity. But I think the real distinction between them is that in the tongue rod the subepithelial portion is usually and typically as thick as the sides, and distinctly continuous therewith; whereas in the primary rod the extra-cœlomic piece (subepithelial) is thinner, and, owing to the greater development of the cœlom here, is more widely separated from the rest of the rod. This suggestion occurred to me forcibly in examining the connections of the synapticula with the two bars.

In a lucky series of sections, cutting the bars very accurately transversely, one often gets the whole synapticulum in sections, passing from one primary bar to the next, and showing the connection of the rod in the transverse bar with those of the main bars (fig. 31). Starting with the tongue bar (*T.*), the rod forks, so that its contained cavity is no longer bounded by a chitinoid wall; one branch of the fork passes towards each of the adjacent primary bars, and is continuous, not with the main part of the rod itself, but with

[1] Spengel gives a figure very similar to this one in pl. xvii, fig. 13, illustrating his paper.

the cutis (basement membrane of Spengel), or extra-cœlomic portion of the rod, as I would regard it. But this apparent forking of the tongue rod is due merely to the passage of the contained blood-vessel out of the rod to the vessels of the adjacent primary bars; so that in reality, as many sections show, the rod of the connecting bar, i. e. the synapticulum, is connected on the one hand with the extra-cœlomic portion of the tongue rod, and on the other with the extra-cœlomic "cutis" of the primary bar.

A second difference between the rods is that the skeletal vessel is inside the cœlom in the tongue bar, but outside it in the primary bar over the greater part of its extent, though, in the lower part of the latter bar, it is intra-cœlomic, as in the tongue bar (fig. 30, *a*). I have sometimes seen a small cavity outside the rod in the tongue bar, but I have not been able to satisfy myself as to its nature; it may be merely artifact.

B. Summary of my Observations and Interpretations.

1. The epithelium of the bar is everywhere only one cell in thickness.

2. The arrangement of the cells at the pharyngeal end of the bar, both in the primary and in the tongue, is much more definite than previous observers, except Lankester, have figured and described; the central group, contrary to Lankester's opinion, presents two rows of nuclei, and carries a bundle of very long cilia; the lateral groups carry quite short cilia.[1]

3. The nuclei at the sides of the bar are oval and not round, and the lowest row has nothing to do with the septal membrane.

4. There are three blood-vessels in the tongue, as in the

[1] This differentiation of the cilia round the bar may be compared with that occurring in the gill filaments of Lamellibranchs, and in the cirri of Brachiopods, where there are similarly bundles of long cilia, situated at the sides or angles, and shorter cilia elsewhere. The existence of a skeletal tissue in these cases is a further analogous resemblance.

primary, bar; (*a*) the visceral vessel at the pharyngeal end of the bar; (*b*) the somatic vessel in the apical notch of the rod; and (*c*) the skeletal vessel inside the rod: the last two anastomose here and there.

5. The cavity of the rod is cœlom, is lined by flat cells, and contains this skeletal blood-vessel.

6. The outer wall of this cœlom is homologous with the extra-cœlomic cutis (Spengel's basement membrane) of the primary bar.

7. The septal membrane and the rod are mesoblastic, and the nuclei of the cells forming them are here recorded for the first time.

c. The Observations of Recent Observers.

I will now pass on to a brief survey of the various descriptions and figures of the tongue bar of previous writers, copies of whose figures are represented on Pl. 6, and in the explanation of these, the references whence the figures are taken. Stieda, Langerhans, and Schneider saw no modifications of the epithelium at the pharyngeal end of the bar. Lankester was the first to observe this, and his figures represent more accurately than do those of his successors, Spengel and Boveri, the actual arrangement. As I have already pointed out, however, he missed the fact that the middle group presents two rows of nuclei. This is equally overlooked by Boveri, while Spengel's drawing is not quite clear on this point, and neither of these latter indicate the much greater length of the nuclei in this part of the bar. So far as the general shape of the pharyngeal end of the bar is concerned, Spengel's and Boveri's drawings show it fairly. Fig. 12 from Boveri is taken from quite the upper end of the bar, hence the peculiar shape of this end. Lankester is alone in regarding—as I believe wrongly—the epithelium of the sides of the bar as in several layers. Spengel points this out; but he, like all my predecessors, with the doubtful exception of Schneider and Langerhans, represents small round instead of oval nuclei here.

The authors, as will be seen from the reproductions of

their figures, represent the characters of the atrial epithelium at the upper end of the bar correctly, with the exception of Langerhans, who describes each cell here as bearing a flagellum.

Stieda and Langerhans did not recognise the differences in the length of the cilia round the bar. Schneider is the first to figure the long cilia at the sides, and the remaining authors follow him. Spengel is the first to note this tuft of long cilia at the pharyngeal end; but both he and Boveri[1] overlooked the short cilia carried by the lateral groups of cells at this end.

With regard to the contained vessels in the primary bar, Langerhans entirely missed the vessel at each end of the septal membrane. Schneider and Lankester saw only one vessel—that at the outer end of the bar at the apex of the rod—the somatic vessel. Spengel most unaccountably missed this vessel, although he states that he looked carefully for one here, and his figure of the tongue bar (Pl. 6, fig. 7) shows a very narrow cleft in its position, whilst he describes the inner or visceral vessel (*vn.*), which is usually less noticeable than the other. In this respect his figure shows no advance upon that of Stieda, who also saw, but did not describe, the space at the inner end of the bar.

Boveri, however, observed this vessel (and figures it) in the primary bar (fig. 12, *ve.* 1), in the position already given to it by Lankester, but overlooked it in the tongue bar (fig. 8). As a matter of fact, as I have stated above, there are three vessels in each bar. Schneider and Lankester found one, the "outer or somatic" vessel; Spengel found one, the "inner or visceral vessel," but denied the somatic vessel. Boveri found both these in the primary bar, but overlooked the "outer vessel" in the tongue bar.

As to the nature of the rod cavity, Stieda and Langerhans leave it aside.[2] Schneider represents (at *A*, fig. 5) "a blood-

[1] It should be borne in mind, however, that Boveri did not pretend to describe the bars except in so far as they are related to the nephridia.

[2] Stieda regards the granular substance in the centre of the rod (fig. 2, *a*) as an axial part of the rod itself.

vessel communicating with the branchial artery." Lankester, from its relation to the subendostylar cœlom, regarded this canal in the rod as "cœlom;" whereas Spengel and Boveri look upon it as a blood-vessel, and deny its cœlomic character. Lankester gives half a dozen figures (loc. cit., pl. xxxvi B, figs. 5—9) of as many consecutive sections representing the canal communicating with the subendostylar cœlom. Spengel denies this altogether, and states that the rod becomes solid before it reaches the endostyle, and there becomes continuous with the subendostylar skeleton. He further denies any communication of this rod cavity with the dorso-pharyngeal cœlom.

Now the tracing of these cavities is an extremely difficult matter, owing to the difficulty of making sections in the right plane, and I searched through section after section before I could satisfy myself as to the mode of termination of these rods. Time after time it seemed to me that Spengel was right, so far as the non-communication of the rod cavity was concerned; but in certain lucky sections I found that the plane was convenient for this purpose, and I represent five consecutive sections which show, as I believe, the continuation of the subendostylar cœlom into the cavity of the rod (Pl. 7, figs. 22—26). The series shows most certainly no continuity between the rod and the subendostylar skeleton on which Spengel insists.

I was not successful in tracing the rod cavity into the dorso-pharyngeal cœlom; but I attribute this to the difficulty of observation, and am by no means inclined to conclude that such a connection does not exist.

The "skeletal vessel" ceases some little way before the rod does, being connected with the vessels in the neighbouring primary bars at the lowest synapticulum.

If the hinder gill-slits be examined in a preparation of the pharynx, flattened out on a slide, and the mode of development of the "tongue" observed, it will be seen that the rod in the tongue is double at its upper end; the two pieces diverge and constitute the arcade connecting the series of rods. The tongue bar, as is known, is a downgrowth from the upper

boundary of a primary slit; the cœlom is here in the form of a canal giving off shoots to each bar, and fro them appearance presented in such a preparation, it is not an inconsistent interpretation to regard the cœlom as sharing in the downgrowth of its ventral wall. The appearance presented by the rod in the hinder gill-slits is thus: M.

D. Certain Abnormal Bars.

In one series of sections the pharynx presented a few bars containing sometimes three and sometimes two rods. In all cases these abnormal bars are "primary" bars, i. e. the rods contained within them are cleft rods, similar to those found in normal primary bars; and on each side of such abnormal bars there lies a normal tongue bar, separated by a pharyngeal slit from the abnormal one. On Plate 7, fig. 27, I represent one such bar cut at about the middle of its length, containing three rods, which are in all respects similar to one another. The bar itself is otherwise normal, and presents the usual characters of the epithelium in its various parts. Naturally the bar is much wider than an ordinary one, especially at its atrial end. The septal membrane (*s.m.*) is very short, but the two usual blood-vessels (*vix.v.* and *som.v.*) are present. There is not a vessel at the apex of each rod, as one might expect; the cœlom is very extensive, and dips in between the rods as the nuclei show. The usual subepidermic blood-vessel (*skel. v.*) is also present. But this bar, if traced upwards towards the epibranchial groove and downwards towards the endostyle, presents variations of this condition in different regions.

At its origin dorsally the three rods are fused together, but this occurs for only a very short space, and we soon find three rods. Towards its lower end two of these (Nos. 1 and 3) are fused, so that the bar has but two rods; and still further a junction between these two is effected (fig. 28), and there appear to be but one rod, rather larger than usual, but evidently consisting of two united rods. Soon, however, these separate again, and I take this union as representing a synapticulum.

But now the relative position of the two rods changes;

hitherto they have been side by side, or rather anterior and posterior; but now (fig. 29) one (No. 2) lies outside the other (Nos. 1 and 3), which occupies the normal position. I was unable to track the rods quite to their junction with the floor of the pharynx owing to the imperfection of some of the sections in this series.

Most of the other abnormal bars contained two rods, but I did not trace them all out from top to bottom, so that I am unable to state whether they always contain, at some part of their length, three rods. But I am inclined to answer this in the negative; so frequently are there only two rods that I think this is the more "usual" abnormality. There is another triple-rod bar on the opposite side of the pharynx, at about the same level as the one described, and usually, as far as I could observe, the abnormal bars are opposite.

A bar with a double rod might conceivably be produced by closure of a primary slit between two primary bars; but there is no evidence of any formation of a slit and subsequent closure and fusion of the bounding bars. One would expect if this had happened that the cœlom and subepidermic vessel would be doubled, and that the pharyngeal end of the bar would exhibit some peculiarity; this I did not find to be the case. A triple-rod bar might be explained by an extension of this suggestion, namely, that two slits had remained imperforate, whilst the rods had been formed nevertheless.

EXPLANATION OF PLATES 6 and 7,

Illustrating Dr. W. Blaxland Benham's paper on "The Structure of the Pharyngeal Bars of Amphioxus."

In most of the figures the blood-vessels are represented black, but in fig. 14 I have drawn the actual appearance presented by the sections.

Figs. 1 and 2.—Transverse sections of a tongue and a primary bar, so far diagrammatic in that each figure is a combination of several drawings of

different sections, which have been treated in different ways. The two figures are drawn to scale, and therefore represent the true relative sizes of the bars.

Fig. 1. A transverse section of a tongue bar of the pharynx of Amphioxus (Branchiostoma lubricum, Costa). It represents, accurately as I believe, a typical section of the bar. Most of the parts are fully named on the plate. The rod contains a cavity—the cœlom, lined by an epithelium, whose nuclei are shown (see also Fig. 13). Within this cœlom lies a blood-vessel—the skeletal vessel. Two other blood-vessels are present in the bar, the "visceral" (*Visc. Bl. vessel*) and the "somatic" blood-vessel; these lie at either end of the septal membrane, between the two layers of which are shown three nuclei (see also Figs. 20, 21). The atrial epithelium consists of only one kind of cell. The grouping of the epithelial nuclei at the pharyngeal end of the bar may be noted.

Fig. 2. A transverse section of a primary bar (see explanation of Fig. 1). Here the cœlom is more extensive, and the "cutis"—or outer wall of the cœlom—is thinner than in the tongue bar. The rod itself is made up of two pieces, meeting along the middle line of the bar, and a third piece wedged between. The skeletal blood-vessel is outside the cœlom, but is in reality surrounded by the rod, i. e. "cutis." The atrial epithelium consists of two kinds of cells (see Fig. 17), viz. *a*, the vacuolated, and *b*, the granular cells.

Figs. 3 to 12 are tracings of figures published by previous observers; the only alterations that have been made are (1) colouring the rod yellow, and (2) filling in with black the spaces regarded as blood-vessels by the authors.

Fig. 3. Copied from Stieda's fig. 6, pl. i. "Transverse section of a branchial plate. *a*. The rod. *b*. Deep layer of the epithelium. *c*. Superficial layer with cilia."

Fig. 4. Copied from Langerhans, fig. 24, pl. xiii. "Transverse section through a gill bar. *m*. Epithelium. *k*. Nuclei of branchial epithelium *p.e.* Pigmented epithelium. *h*. The atrial epithelium. *s*. Hollow gill rod."

Fig. 5. Copied from Schneider's fig. 4, pl. xiv. "Transverse section of a thin (that is, tongue) gill bar. *a*. Triangular space, a blood-vessel. *A*. A blood-vessel in communication with the branchial artery. k^1. The rod. *p.p.* Peritoneal (i. e. atrial) plate."

Fig. 6. Copied from Lankester, pl. xxxvi B, fig. 2. "Transverse section of a tongue bar. *al.* Left inner epithelial band. *ar.* Right inner epithelial band. *am.* Median inner epithelial band. *col.* Columnar lateral cells, with long cilia. *n*. Superficial nuclei. n^1. Deeper nuclei. *sept.* Clear septal tissue. *Bl. v.* Supposed blood-vessel, ending blindly at the ventral extremity. *pig.* Lateral groups of pigment in the atrial epithelium. *at. ep.* Atrial epithelium (epidermic)."

Fig. 7. Copied from Spengel, fig. 19, pl. xviii. "Transverse section of a tongue bar. *vz.* Chief vessel of the bar. *vn.* Accessory vessel."

Fig. 8. Copied from Boveri's fig. 14, pl. xxxiii. "Transverse section of tongue bar at the level of the nephridium. *neph.* Position of nephridium. *vi*[II]. Inner axial vessel. *ve*[II]. Outer axial vessel."

Fig. 9. Copied from Schneider, pl. xiv, fig. 3. "Transverse section of a thick (i.e. primary) gill bar. A^1, A^2. Blood-vessels which are in communication with the branchial artery. *a.* Triangular space, blood-vessel. *p. p.* Peritoneal (i.e. atrial) plate. *V.* Vein in communication with the subvertebral vein, and the venous space around the branchial artery. k_2. The thick rod."

Fig. 10. Copied from Lankester, pl. xxxvi B, fig. 1. "Transverse section of a primary bar. *B.v.* Blood-vessel connected with the lateral branches of the median endostylar vessel. *fiss.* Fissure due to the bilateral origin of the rod. *cœ. ep.* Cœlomic epithelium. *pg.* Pigmented atrial epithelium."

Fig. 11. Copied from Spengel's fig. 12, pl. xvii. "Outer part of a transverse section through a primary bar. *b. m.* Basal membrane. *cök.* Cœlomic canal of the bar. *sp.* Skeletal rod. *vk.* Chief vessel in the primary bar."

Fig. 12. Copied from Boveri, fig. 6, pl. xxxii. "Transverse section of a primary gill bar, *vi*[I]. Inner axial vessel. *ve*[I]. Outer axial vessel. *vc.* Cœlomic vessel. *cœ.* Cœlom."

Fig. 13.—A tongue rod in section, to show the skeletal blood-vessel (*sk. b. v.*) running in a special canal; it is probably about to anastomose with the somatic vessel (*som. b. v.*). Around the cœlom (*cœl.*) three nuclei (*n. c. ep.*) are present, embedded in granulations (? protoplasm). In this section the two blood-vessels, as is frequently the case in cochineal preparations, are stained deep red. The cœlom is quite clear. *cu.* cutis.

Fig. 14.—A rod from a tongue bar, exhibiting granulations in the cavity, which are of two kinds: a coarser, less deeply stained, in the outer part, which is probably the protoplasm of cœlomic epithelium—in that region marked *cœ.*—cœlom; and a finer and more deeply staining mass (*skel. b. v.*), the skeletal blood-vessel. The two are apparently separated by a partition. *n.* is the nucleus of the cœlomic epithelium. *som. b. v.* The outer or somatic blood-vessel. *cu.* The "cutis" or outer wall of cœlom. From a preparation stained with Mayer's alcoholic cochineal. Drawn under Zeiss's homogeneous immersion.

Fig. 15.—A modification in the shape of the section of the rod, which is not unusual, especially near the synapticula. The rod is here composed of two pieces. The outer wall of the cœlom is free of skeletal tissue (cf. Fig. 31), and the blood-vessel (*skel. b. v.*) is passing out of the cœlom (*cœl.*), and lies just below the atrial epithelium (*at. ep.*).

Fig. 16.—Another modification in the tongue bar, which occurs near the upper end of a bar.

Fig. 17.—Cells from the atrial epithelium of a primary bar, from a partially macerated section (cochineal). *a*. Vacuolated cells. *b*. More granular, narrower cells, the nucleus being near the free end. *c*. A portion of a cell, which is probably similar to *d*, with a narrow peripheral portion, and dilated nuclear region below.

Fig. 18.—Three cells of the atrial epithelium of a tongue bar, from a partially macerated section.

Fig. 19.—Cells from the lateral epithelium of a gill bar, from a partially macerated section. The nuclei of the cells are seen to be at different levels. Each cell carries a single long cilium. The small cell to the left may be a portion of a larger cell, or may be really a basal interstitial cell.

Fig. 20.—A small piece of the septal membrane, with a nucleus (*n*.) (from a transverse section of a bar). The membrane appears to be double, and the nucleus lies between the two sheets.

Fig. 21.—A portion of a longitudinal section of a bar, showing the septal membrane and three elongated, compressed nuclei (*n*.). Only a small portion of the epithelium of the bar is filled in, in order to show the relative size of the nuclei of the septal membrane and those of epithelium (*ep*.). (Hæmatoxylin. Under Zeiss's apochromatic 4 mm., aperture ·95, with compensating ocular 8.)

Figs. 22—26.—Five consecutive sections to show the passage of a tongue bar into the endostyle, and the communication of the rod cavity with the subendostylar cœlom.

Fig. 22. Transverse section of the endostyle and a neighbouring tongue bar. The details as to arrangement of nuclei are only approximately accurate. It is merely desired to exhibit the general topographical relations of the structures. *end*. Endostyle. *end. sk*. Subendostylar skeleton. *end. cœl*. Subendostylar cœlom. *cœ. ep*. Nuclei of the cœlomic epithelium. *at. ep*. Atrial epithelium. *art*. Subendostylar artery. *P*. The lowermost part of a primary bar fused with the endostyle. *x*. The peculiar tissue of elongated vacuolated cells (not reticular tissue). *T. T*. Tongue bars. *rod*. The contained hollow rod; on the left the bar has already reached and fused with the subendostylar tissue, on the right it is still free.

Fig. 23. The next section. The rod of the tongue bar on the left appears to have a narrow cleft in its wall, so that its cavity communicates with the subendostylar cœlom; but this is not so distinct as in the case of the right rod in Fig. 26. (The lithographer has exaggerated this cleft.)

Fig. 24. The right portion only of the next and following sections is drawn. Here the rod of the tongue bar (*T*.) is distinctly smaller, and approaches the corner of the subendostylar cœlom.

Fig. 25. The rod has passed further into the subendostylar tissue, and lies above the corner of the cœlom.

Fig. 26. The cavity of the rod communicates with the subendostylar cœlom most distinctly.

Figs. 27—29.—Transverse sections of an abnormal primary bar at different levels.

Fig. 27. Section about the middle of the length of the bar. The epithelium and general structure of the bar is normal, but contains three separate primary rods, 1, 2, 3, each partially surrounded by a layer of cœlomic epithelium. *visc. v.* The visceral blood-vessel. *som. v.* The somatic blood-vessel. *s.m.* The very short septal membrane. *cœ.* Cœlom. *skel. v.* Extra-cœlomic skeletal blood-vessel.

Fig. 28. A section of the same bar lower down. There are here only two rods, partially fused; the rod to the right is formed by the fusion of rods 1 and 3 (in Fig. 27).

Fig. 29. The same rod lower down, nearer the endostyle. The two rods have separated again, but have shifted their relative positions.

Fig. 30.—Three sections of a normal primary rod at different levels. (*a*) Close to the endostyle, where it consists of two independent pieces. (*b*) Slightly higher up, where a third piece (sometimes isolated) plugs the gap between the two pieces, with which it is more or less fused. (*c*) The general condition, in which the fusion of the three pieces is complete, except for a narrow axial cleft (? or less refractive substance). *R.* The rod, in the usual sense. *cu.* "Cutis," or outer wall of cœlom. *cœ.* Cœlom. *skel. b. v.* Skeletal blood-vessel. *som. v.* Somatic vessel. (Cf. Figs. 13—16.)

Fig. 31 *a*.—The connection of synapticulum with the primary and tongue bars. The section is accurately transverse, and includes three bars and the synapticulum. P^1, P^2. The two primary bars. *T.* The intervening tongue bar. *syn.* To the left, half a synapticulum cut along its whole length, and continuous, as is seen, with one half of the tongue rod and the extra-cœlomic "cutis" (*cu.*) of the primary rod. syn^1, syn^2. The two portions of the other half of the synapticulum (the intervening portion is in a section not figured). $b.v^1$. The subepidermic skeletal blood-vessels of the primary bar. $b.v^2$. The skeletal vessel of the tongue bar, which is seen to divide into a right and a left branch, which fall into $b.v^1$. of the primary bars. *cœ.* Cœlom of the primary bar.

Fig. 31 *b*.—The next section of the primary bar (P^2) showing the passage of syn^2. into the cutis (*cu.*). Other letters as in Fig. 31 *a*.

Fig. 1.

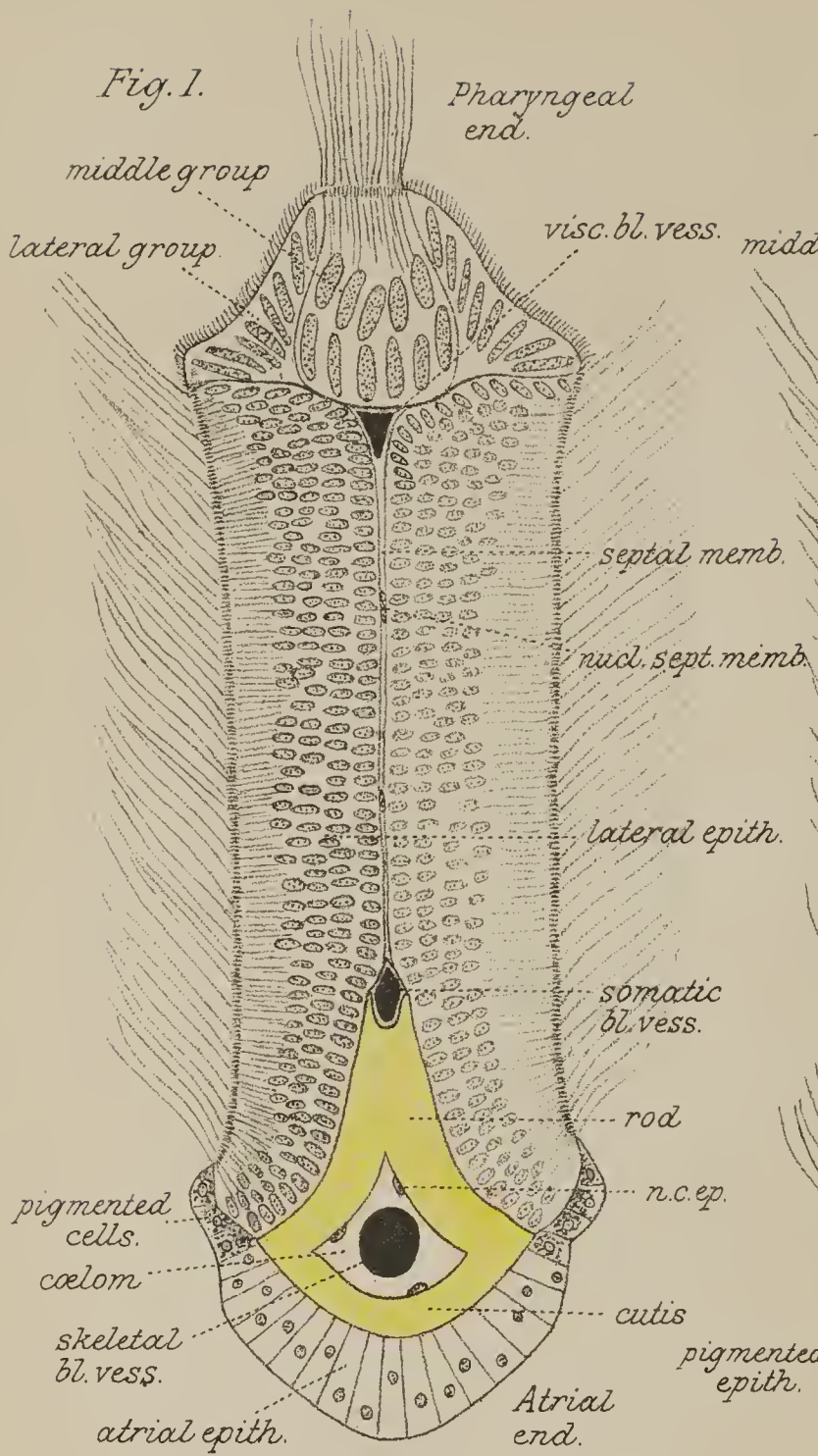


Fig. 2.

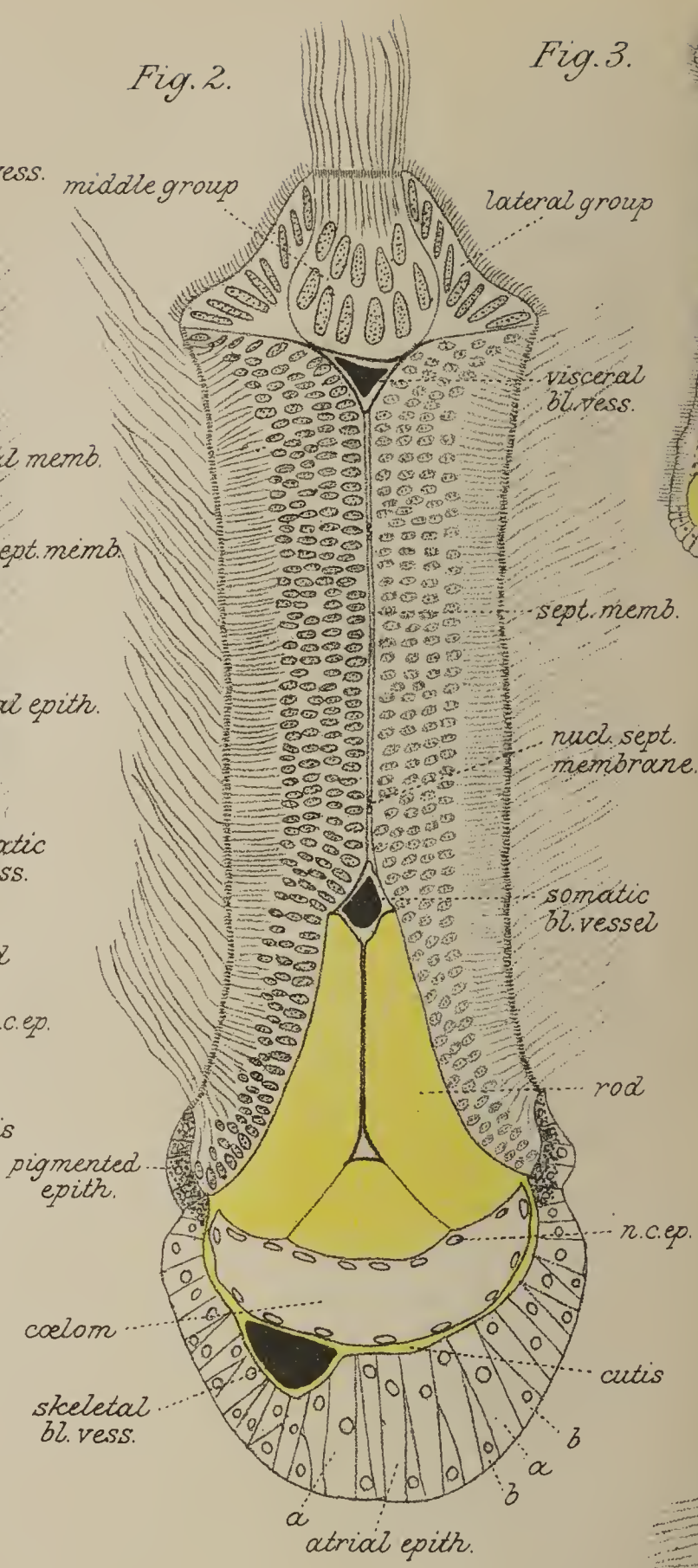


Fig. 3.

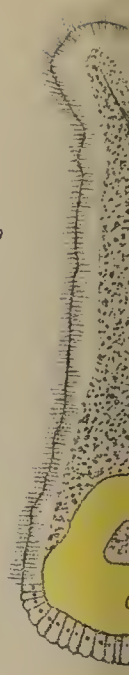
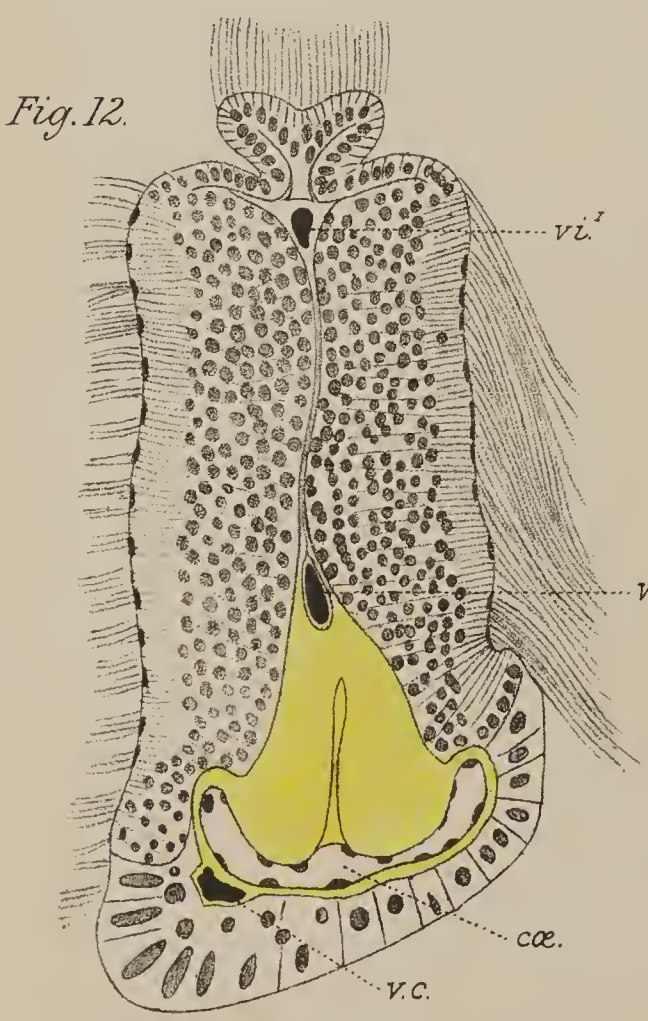
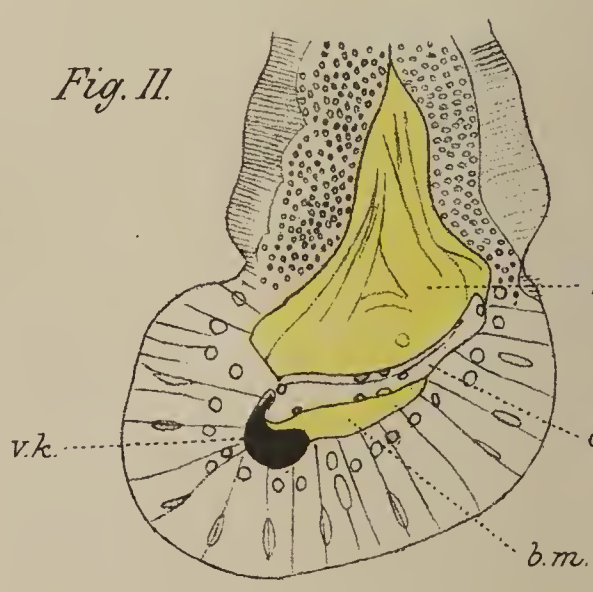


Fig. 12.



BOVERI.

Fig. 11.

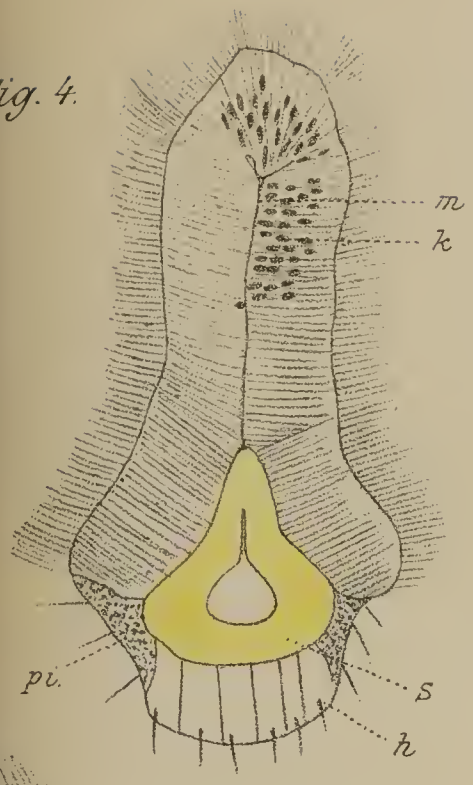


SPENGEL.

Fig. 8.

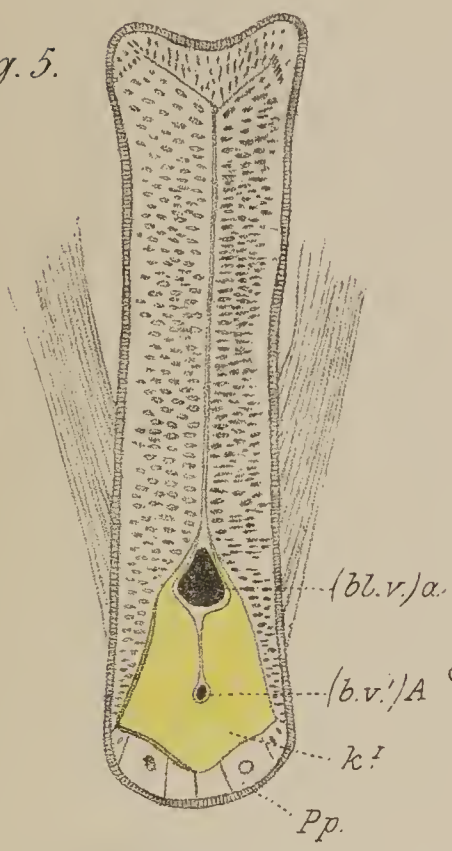
W.B. Benham del.

Fig. 4.



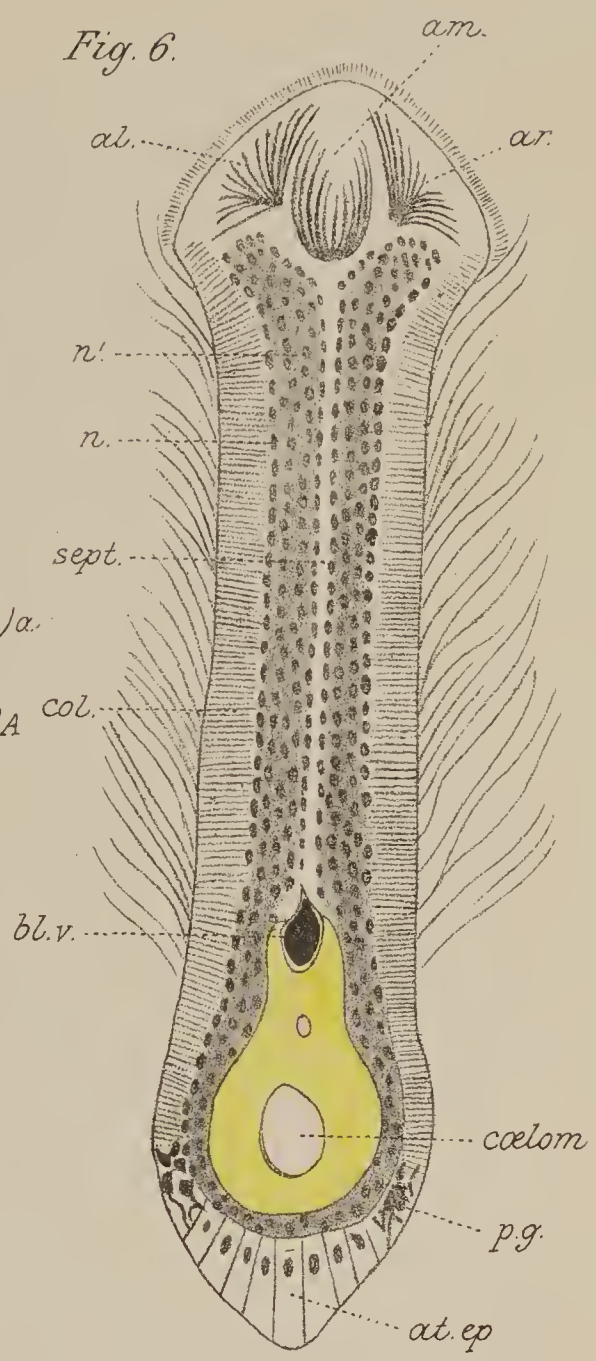
LANGERHANS.

Fig. 5.



SCHNEIDER.

Fig. 6.



LANKESTER.

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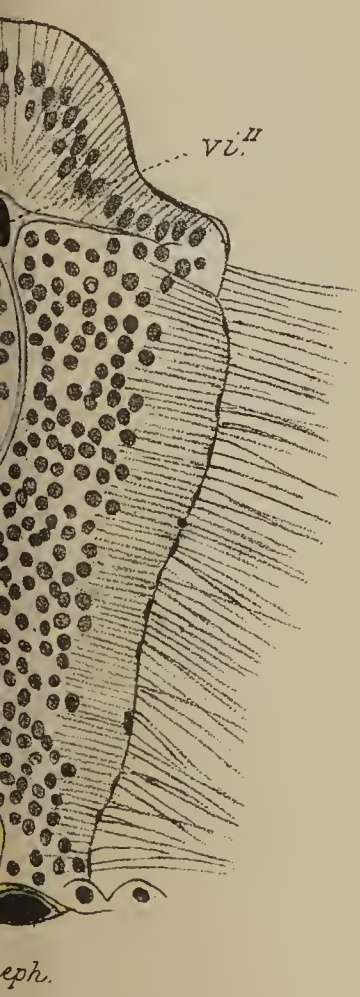

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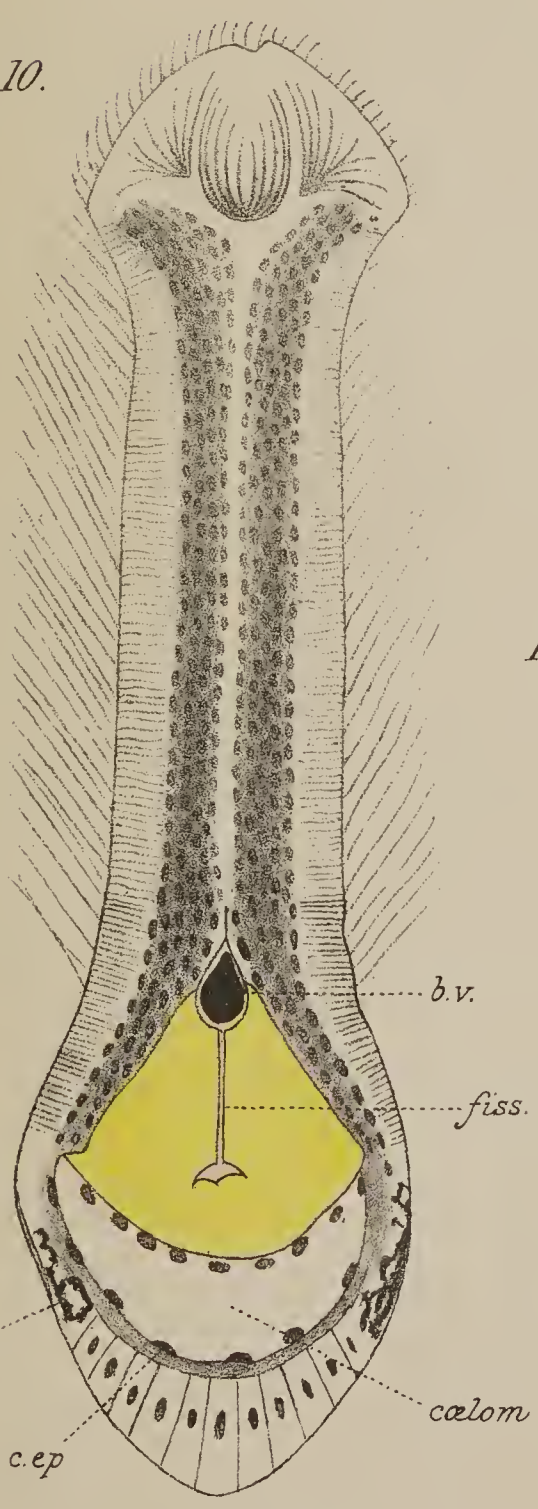
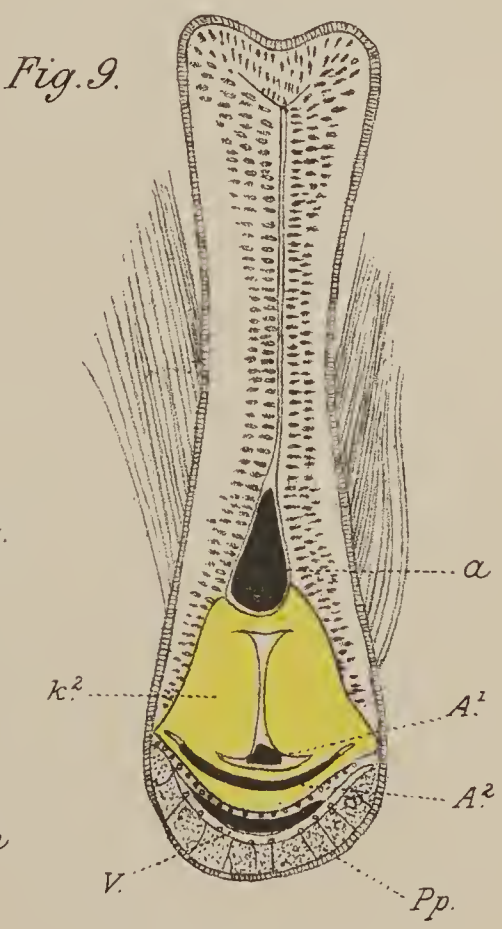
Fig. 10.



LANKESTER.

Fig. 9.



SCHNEIDER.

F. Huth, Lith.r Edin.r

Fig. 13.

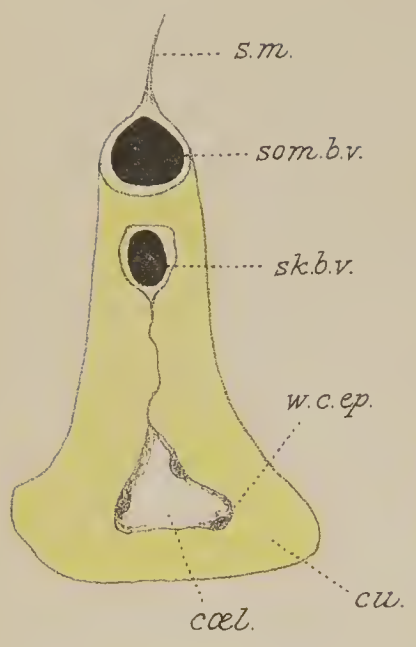


Fig. 14.

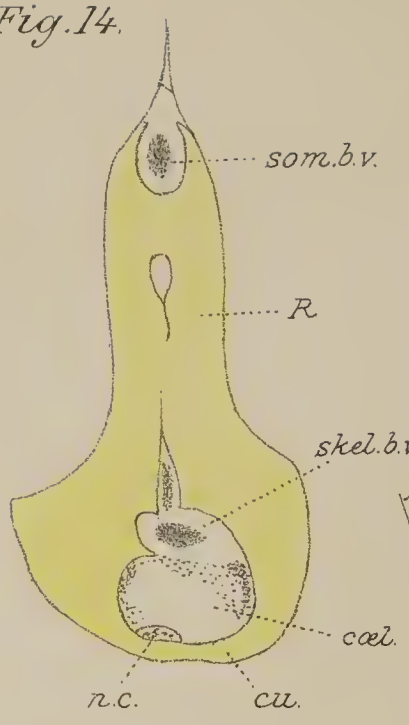


Fig. 15.

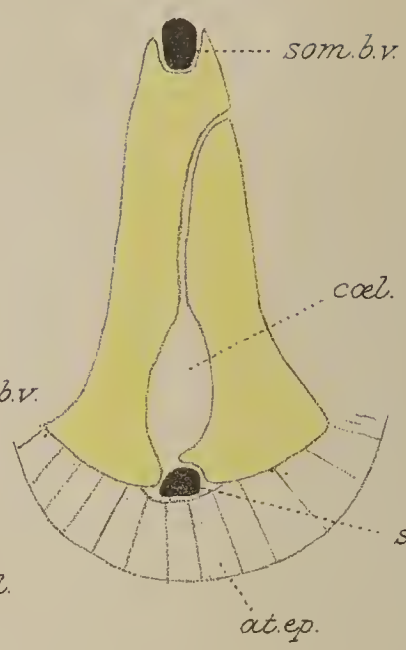


Fig. 16.

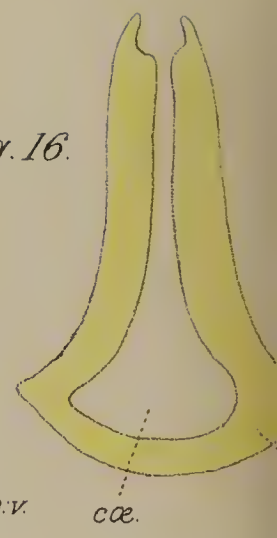
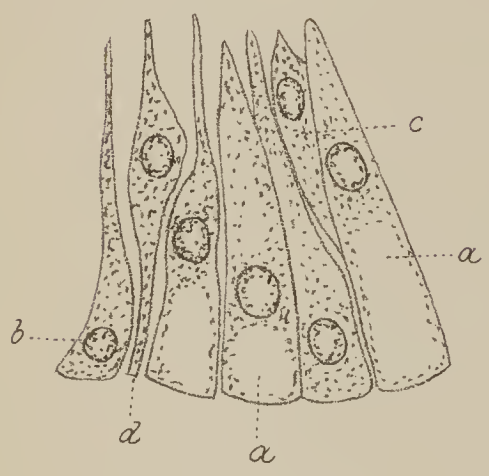


Fig. 17.



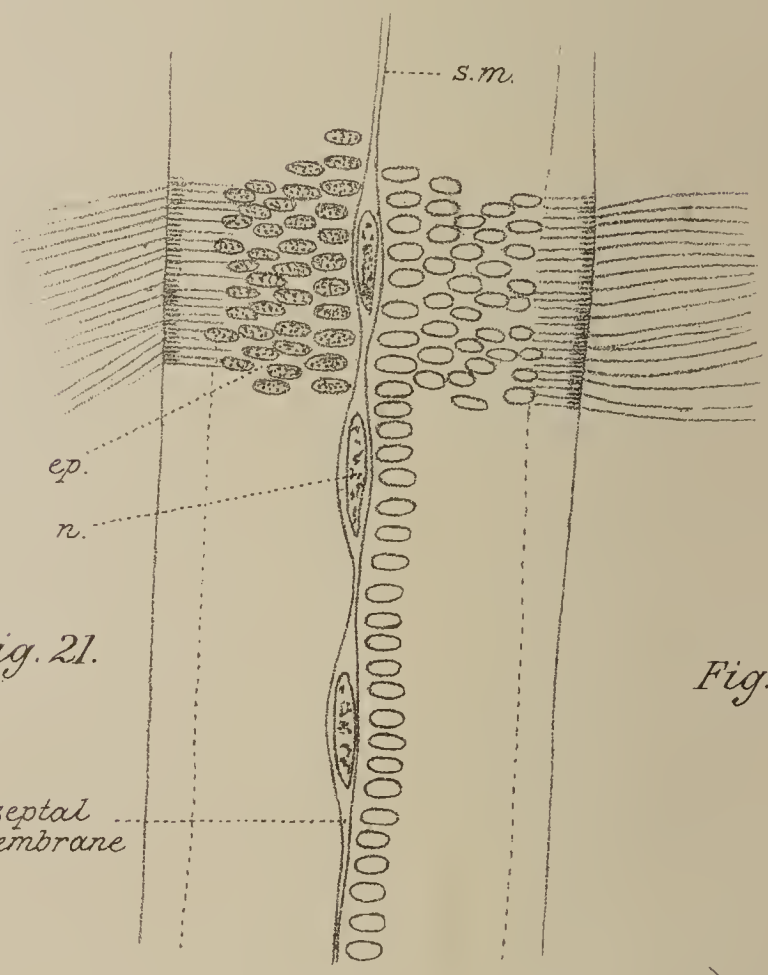


Fig. 18.

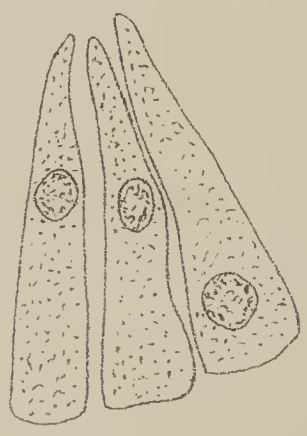
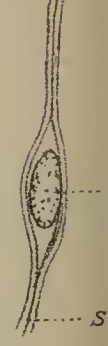


Fig. 21.

Fig. 20.



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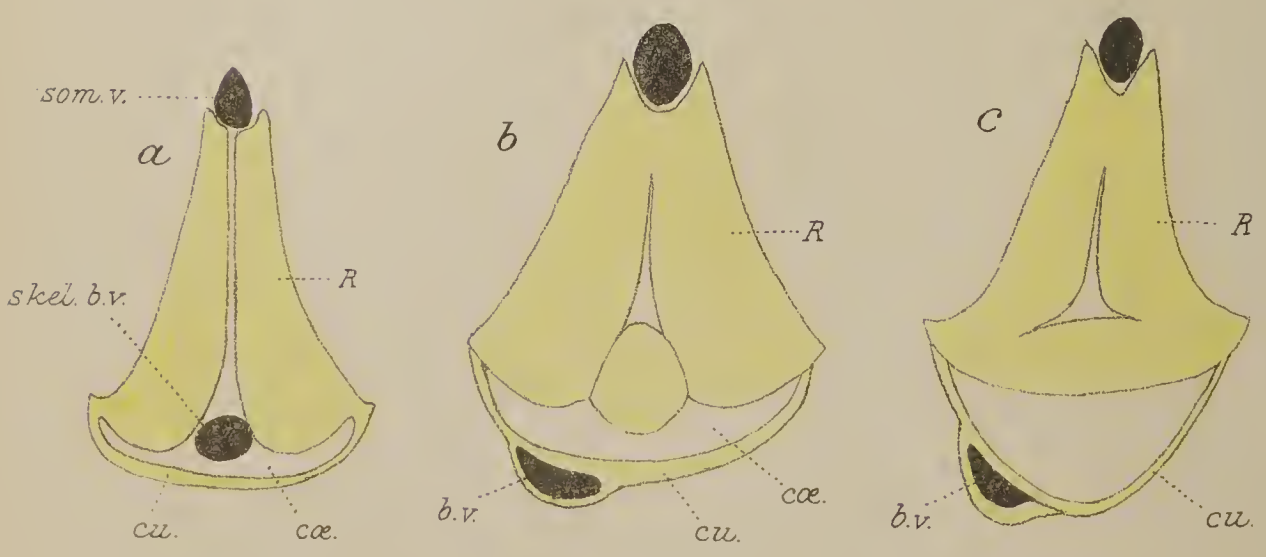
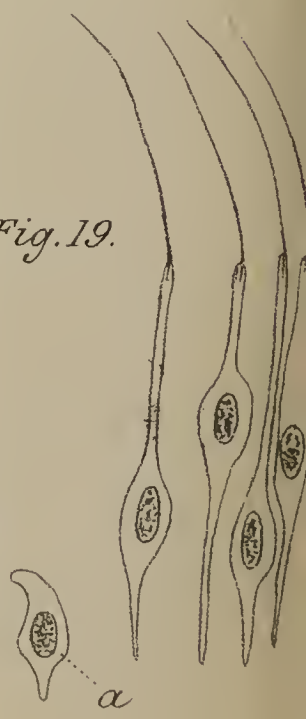


Fig. 19.



W. B. Benham del.

Fig. 31.

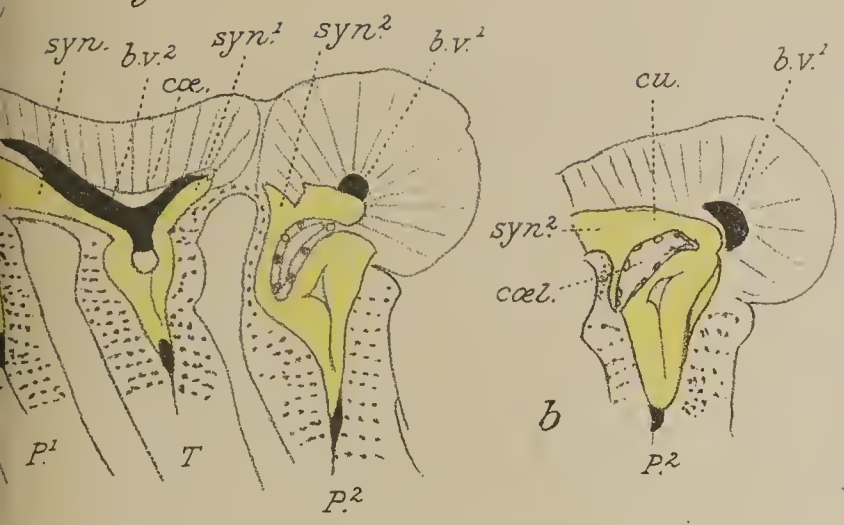
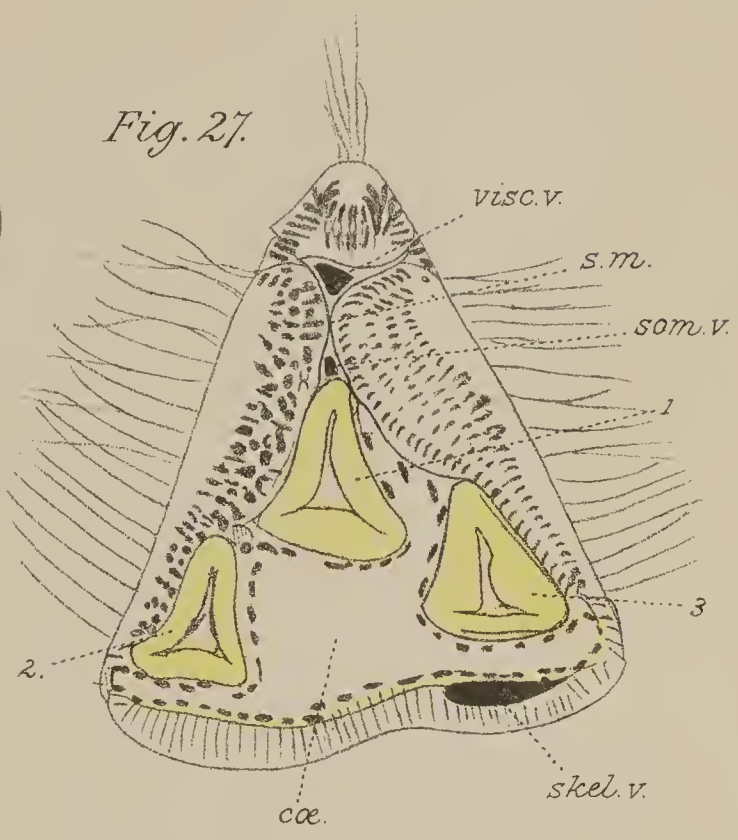


Fig. 27.



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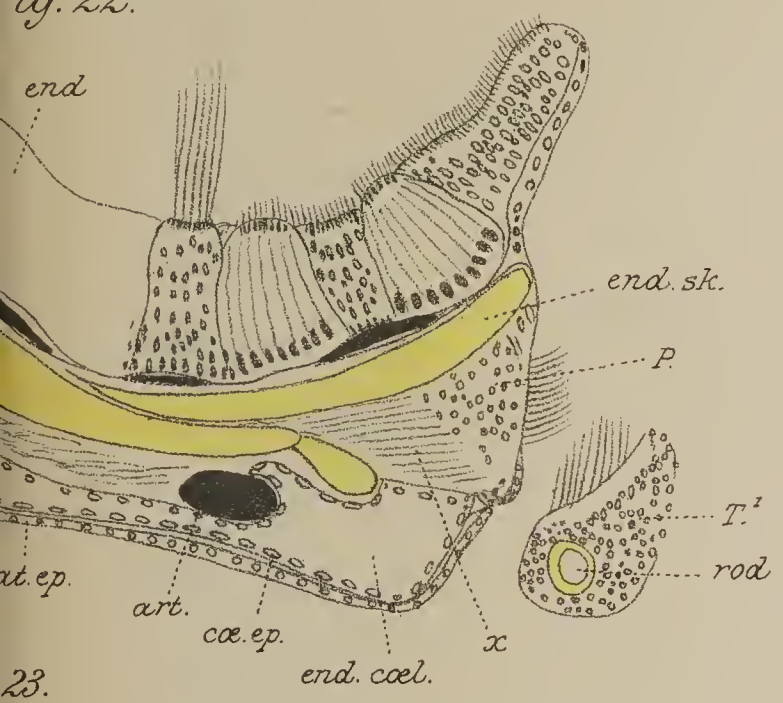

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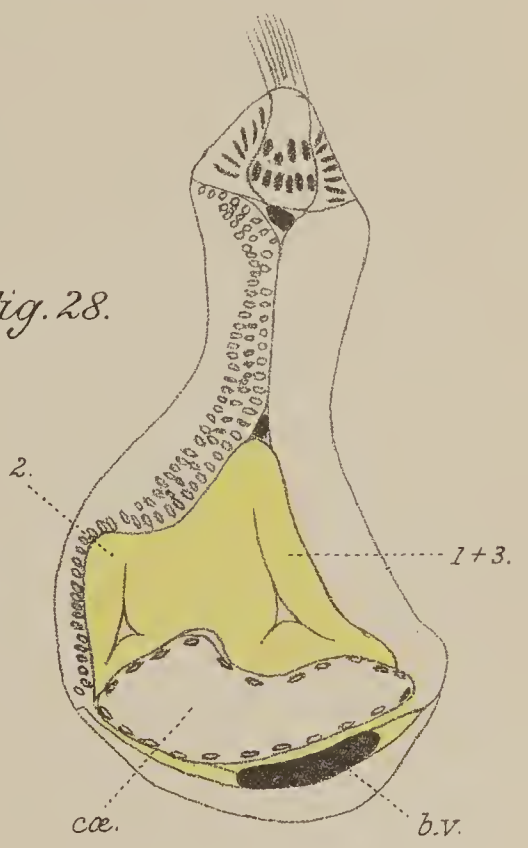

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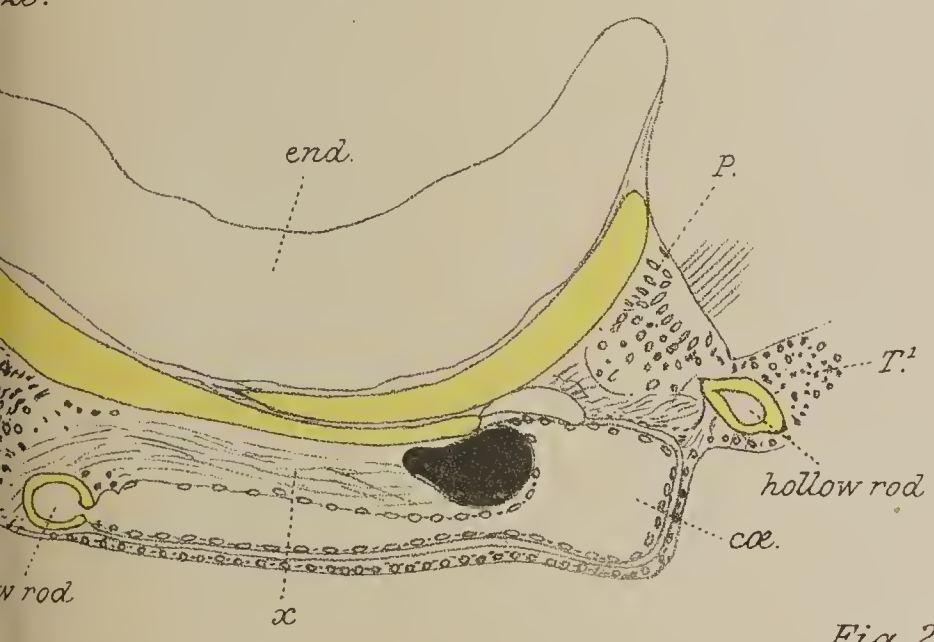


Fig. 29.

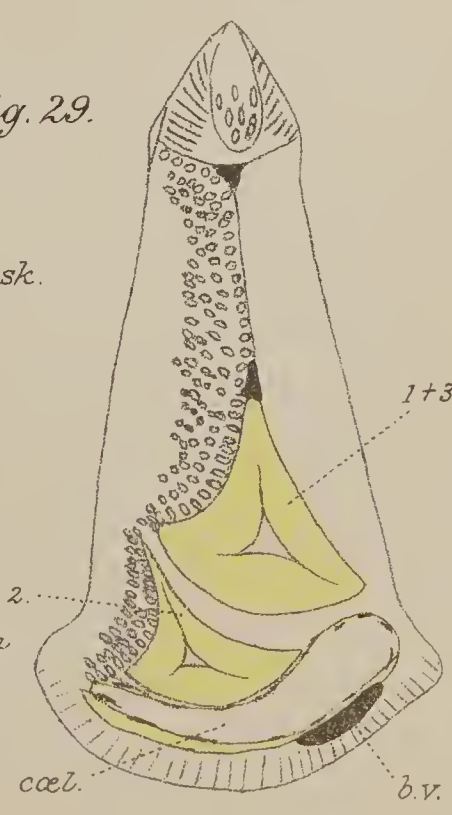
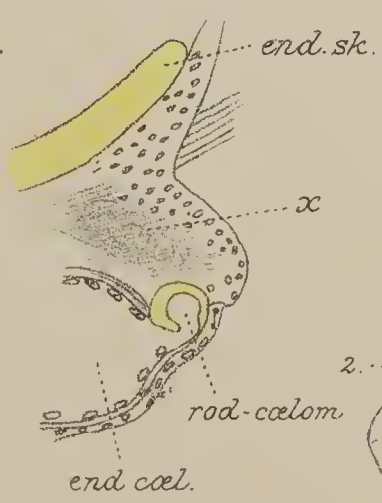


Fig. 26.



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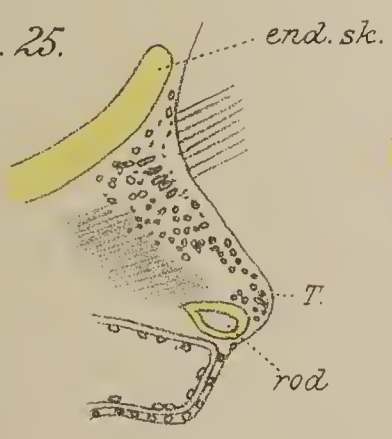

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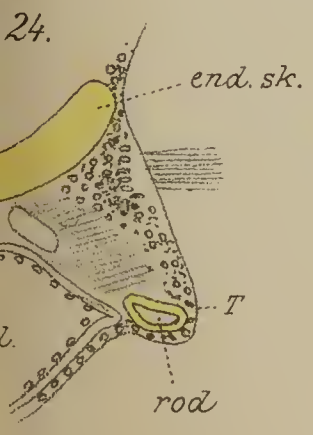


F. Huth, Lith.r Edin.r

The Interlocking of the Barbs of Feathers.

By

W. P. Pycraft, M.B.O.U.

The exquisitely beautiful and remarkably modified epidermal products, which we know as feathers, have probably received more attention than any other form of clothing in the animal kingdom. Science, Commerce, Poetry, Art, and Fashion have each in turn laid them under contribution ; a fact which, it will be readily admitted, has been beneficial to all but those most immediately concerned—their possessors, the birds.

Now we have just implied that feathers are structures with which the world in general is tolerably familiar. To a certain extent this is true; nevertheless I have ventured to present the readers of 'Natural Science' with what I hope will prove a concise account of the mechanism by which the characteristic unity and elasticity of the vane of a typically perfect feather is secured, believing that this will be received not altogether as stale news. I wish it, however, to be distinctly understood that, for the most part, what I have to say will be found little else than a restatement of a tale already told, though in one or two somewhat minute points my claim to originality will, I believe, be allowed to pass unchallenged. These "points" are the results of a careful re-investigation of the question now under discussion, carried on at the instigation and under the direction of Professor E. Ray Lankester, in the Department of Comparative Anatomy of the University Museum, Oxford.

Before proceeding to the more special subject of this article, it may be well to direct attention briefly to the accompanying diagram of a feather (Fig. 1). There may be noted (1) the

strong pliant scapus or stem (*Sc.*), divided for convenience' sake into two parts, (*a*) a rachis (R_1) or distal, and (β) a calamus (C.)—commonly called the quill—or proximal portion; and (2) the rami or barbs (R^1), lanceolate processes, seated in two rows, one on either side of the rachis, and pointing to the tip of the feather. The interstices between the rami, it will be observed, are filled by exceedingly numerous and very small processes, looking to the unaided eye in the natural feather more like bristles, perhaps, than anything else; these are the radii or barbules (R.), and it is mainly with these that we have to deal in explaining the structure of the vexillum (V.) of a feather. The vexillum, it must be remarked, is the compact, well-knit, elastic fringe or web ("beard," as it is called in German), composed of rami and radii interlocked in a manner to be described presently.

It has just been remarked that the interstices between the rami are filled up by exceedingly small processes called radii; of these there will be found two rows to every ramus, one directed towards the tip of the feather—the distal series—and one looking towards its outer or inner edge, as the case may be, and neither to the tip nor the base of the feather, as has been described. Now if we press a sharp knife along the edges of one of these barbs, we shall succeed in getting a number of radii of two quite distinct varieties, though they have this much in common, both may be likened to lamellæ which have undergone the process familiarly known as "warping," in a longitudinal direction. Those of the distal series (Fig. 4) are found to be lamellate for about half their length, when the lamella might be imagined to have been cut up into a number of long, slender, filiform processes, some of which are hooked at the tip. If hooked, they are called hamuli, otherwise they are commonly known as cilia. The hamuli are confined to the ventral edge of the radius, but the cilia may occur on both dorsal and ventral edges.

The radii of the proximal series will be found, in addition to the warping, to have their upper edges folded somewhat sharply over towards the hollow surface, as in Fig. 3. After

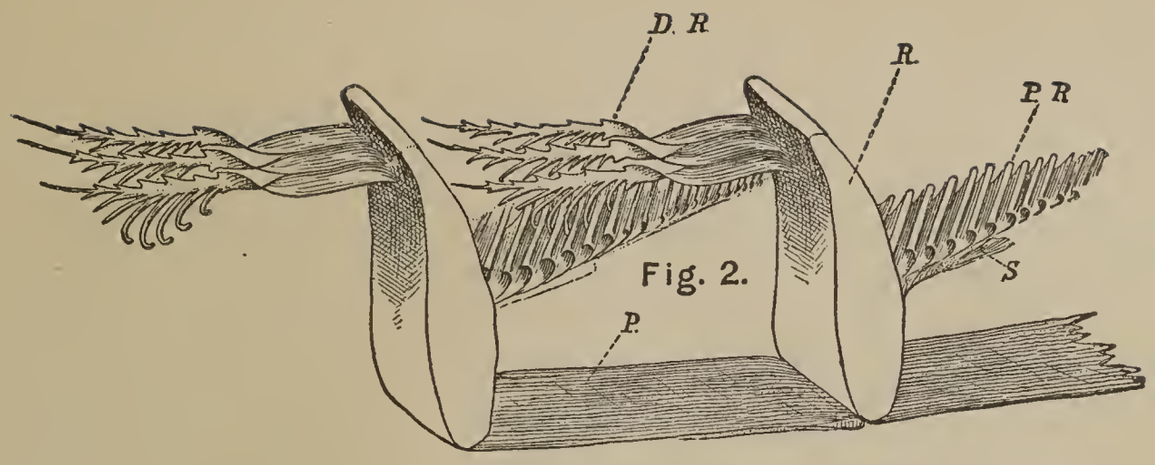


Fig. 2.

Section through 2 rows parallel to the distal Radii.

D. R. Distal Radii P. R Proximal Radii

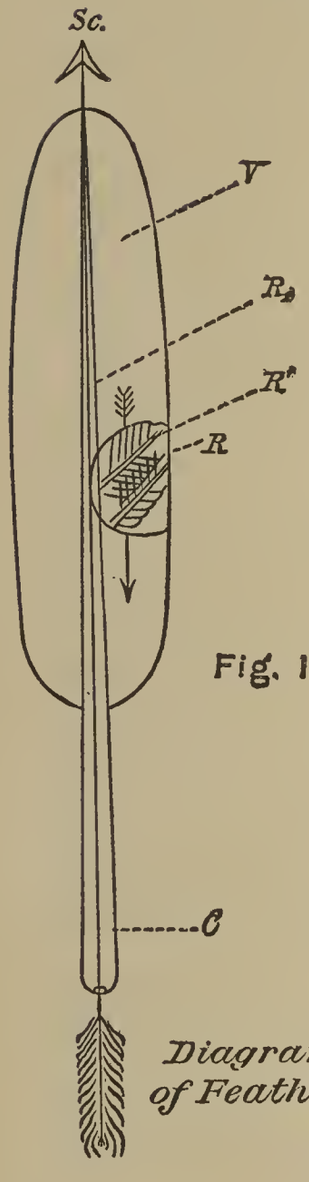
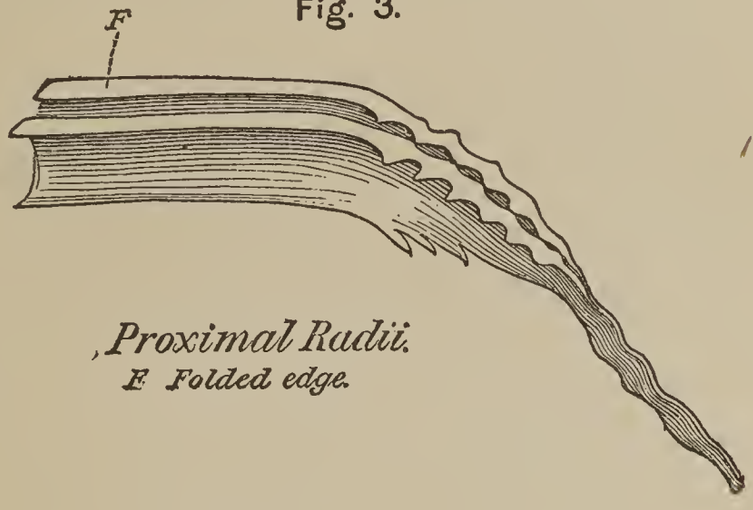


Fig. 1.

Diagram of Feather.

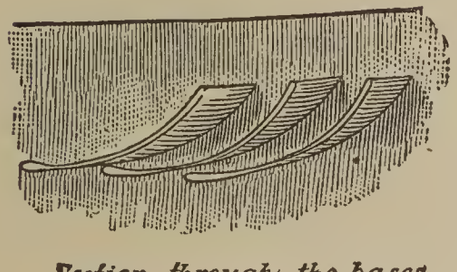
Fig. 3.



Proximal Radii.
F Folded edge.

Fig. 4.

A Distal Radius
H. Hamuli or Hooklets.
C. Cilia or Barbicels.



Section through the bases of 3 Distal Radii

Fig. 5.

Fig. 6.

Magnified Section through a Hooklet and folded edge of a Proximal Radius.

F. Folded edge.
H. Hooklet.

rather more than half of its length, this edge gives place to a series of notches, which soon—rapidly diminishing in size—blend with the almost and often quite filiform tip, into which the distal moieties of these radii are produced. It must here be noticed that, in the region of the notched edge, the radii are bent at a slight angle upon themselves, the bent ends being closely approximated, as shown in the figure.

So much for the general conformation of the radii. What is the reason for this warping? and what is the actual method of interlocking? are questions that my readers will here naturally ask.

Probably a glance at Fig. 2 will explain more than could ever be done by mere description. Here we have a semi-diagrammatic representation of an oblique section across two rami (R.), taken parallel with the distal radii, or what amounts to the same thing, parallel with the shaft of the feather (P.). As I have hinted, the figure tells its own story, but I should like to draw attention to the following details.

It will be observed in Fig. 2 that the proximal halves of the distal radii appear as flattened, overlapping laminæ, which at about the middle of their length suffer a sudden twist in a vertical direction, then breaking up into the hooklets and cilia previously described. These hooklets, it will be seen, are thrust down between the scroll-like upper margins of the proximal series, between which there is only just room enough to allow the hooklets to pass. The proximal radii are somewhat puzzling, perhaps, because seen in section; this, however, is unavoidable, as a reference to the diagram, Fig. 1, will, I think, make clear. The true relation of this series having been grasped, there is little else to note for the moment, except the folded upper edge, whose function is obviously to afford a secure hold to the hooklets just described as being thrust down between them; and the formation of comparatively deep channels by the approximation of their lower edges. These channels are not maintained far, if at all, past the most proximal hooklet; from this point, it will be seen, these sectionised radii diminish in size, terminating

close against the surface of the next ramus.[1] Now it only remains for the reader to draw upon his imagination to see at once that a comparatively severe strain would have to be exerted upon the rami to pull them apart, and if he will only make the experiment on some large quill feather he will be amply satisfied; then let him sever a few rami at their base, and see how easy it is to separate them by pulling the ends in opposite directions, the hooklets, of course, gliding along the grooved edges.

Now a word as to the "warping." The radii of both distal and proximal series are, it will be remembered, longitudinally curved, or "warped," as I have termed it, but in Fig. 2 the radii have the appearance of flattened, not curved laminæ! How is this? Well, I have chosen to give the appearance they present under the microscope when seen in situ, rather than avail myself of the licence allowed me in adopting a semi-diagrammatic figure, for the sake of those who take up this work for the first time; for unless seen in section, it is difficult, if not impossible, to consider these anything but what they appear—flattened lamellæ, seated obliquely along the ramus, and even examination under high powers does not reveal the true state of things. Their actual form appears in transverse section as in Fig. 5, which represents three radii cut off close to their base.

As touching the "channels" of the proximal series, what we have now to do is not so much to tender a reason for their formation—this being rather too presumptuous—as to offer a suggestion to that end. The first thing that will occur to the thoughtful reader is, if these edges were free, and directed straight downwards, might they not be a source of danger to the hooklets, inasmuch as the latter would perhaps frequently catch their lower instead of their upper edges? while the present arrangement suggests a twofold purpose: firstly, to afford

[1] These diminished portions, it should be noted, are the distal ends of radii arising nearer the proximal end of the ramus. A moment's reflection will show—bearing in mind their oblique direction—how that, being placed one in front of the other, the sections will gradually decrease.

a windproof surface for the downstroke of the wing (in the case of the remiges and flight feathers), thus preventing the displacement of the hooklets by the upward rush of air; and secondly, to conduce to that marvellous elasticity of the feather we paused to admire in the earlier part of this paper, the hooklets gliding freely over the smooth, hollow surface, yet with difficulty letting go their hold. Surely there seems to be good reason for these views. At any rate, just such an interpretation as this seems to find favour with so good an authority as Dr. Gadow. I find on reference to his most valuable work the following remarks, which, by the way, however, leaves us in a little uncertainty as to whether the full extent of the curvature of the radii is appreciated or not. Thus (quoting Klee) he says, "Ihr *oberer Rand*[1] ist einfach umgeschlagen, wodurch längs dieses Randes eine vollkommene Rinne zu Stande kommt, die unter dem Mikroskop allerdings den Eindruck eines verdickten Randes macht." And again, speaking of the elasticity of the feather, he says, "Zugleich ist die Fahne in höchsten Grade elastisch, nicht nur durch die Elasticität aller einzelnen Federtheile, sondern weil die Hacken auf den glatten Strahlen *Kanten*[1] hin—und hergleiten können."

The relative position of the radii, like their form, varies. Both distal and proximal rows may arise from what would otherwise be the ridge of the ramus, or the distal radii may arise from the upper border of the ramus, while the proximal may run along quite near the lower border. Frequently the distal radii are overhung by a projecting ledge, formed by the much-compressed ridge of the ramus, and between these every possible gradation may be found, according as the part examined be from the primaries, secondaries, or coverts, or from the inner or outer margins of the vexillum.

Along the lower edges of the rami in Fig. 2 will be noticed a thin transparent band (P), of a width corresponding to the section. This I recently found in the remiges of a Teal (Querquedula crecca). The free edge may be either closely approximated to, or even fused with, the lower edge of the

[1] The italics are mine.

next ramus. To the naked eye this appears along the side of the shaft as a narrow band of silvery whiteness, and very smooth, but I am at a loss to account for its function, and do not care to hazard a guess. I have indicated the presence of a similar band under the proximal radii; it seems, however, to occur but rarely. Mr. R. S. Wray, to whom we shall have occasion to refer presently, makes mention of such a band in his paper, shortly to be noticed.

I propose now to present a sort of census of opinion as to how the "Interlocking of the barbs of a Feather" was obtained; but, to be brief, it will be well to confine attention to the descriptions of some three or four writers whom we may consider to have been more or less well qualified to speak on this subject. This will carry us back some sixty years, to the time of the great Nitzsch, the father of the science of Pterylography. His description was fairly accurate; the wonder is it was not quite so. He perceived that the radii could be divided into two series—an anterior and a posterior, as he called them, but he failed in his endeavour to explain their mutual relations, considering that the hamuli of the anterior radii were for the purpose of catching into "little pits" prepared for their reception in the proximal radii. Burmeister, editing Nitzsch's work a few years later, exploded this theory, and gives essentially a correct explanation. He says, "I have noticed in all parts a strongly thickened superior margin, of such a size that the hooklet can just grasp it. It is behind this margin . . . . that the hooklets take hold."

Owen, writing some thirty years later, gives a much less truthful description. He says, "The barbules arising from the upper side of the barb, or that next the extremity of the feather, are curved downward or toward the internal surface of the shaft; those which arise from the under side of the barb are curved in the contrary direction, so that the two adjoining series of hooked barbules lock into one another in a manner which has been compared to the fastening of a latch of a door into the catch of a doorpost.

Huxley's description is as follows:—"The barbules may be

laterally serrated, and terminated by little hooks which interlock with the *hooks* [1] of the opposed barbules."

The last and most authoritative account is that of the late Mr. R. S. Wray. Practically, his paper, short though it is, tells us all that is to be told; but the author presumably failed to appreciate, or missed entirely, one or two of those nice little differences that will so often escape the notice of the most painstaking workers, of whom he was one. Possibly "'tis a rule in nature," in order that those who come after us may have something left to do.

As just stated, Wray's figures and descriptions may be held in all but a few details to be correct. Exception is taken to his interpretation of the proximal radii. These he describes as ". . . thin laminæ, with a thickened upper edge forming a small ledge or kind of flange;" and continues, "If a single barb be examined, the proximal barbules appear . . . at their proximal end to join on to an edge-piece running parallel to the barb. . . . This edge is seen to be formed by the attenuated halves of these barbules overlapping one another, and being turned at a considerable angle upon the other half." On referring to his figures, however, we find these barbules represented as perfectly flat laminæ, vertically inserted by their base along the ramus, and with a slight "flange" running along the upper edge, but with no trace of the "attenuated halves overlapping one another." True, this is a diagram, but surely it would have been more correct to figure them as more or less scroll-like, than as vertically compressed lamellæ having a "thickened upper edge," since the essence indeed of a diagram is to give us the points of a structure, divested of all superfluous detail. So far as my experience goes, this edge-piece occurs but rarely, neither do I believe it is formed as Wray imagined it, since, in the only case in which I ever found it, the radii were normally related, "the edge-piece," though closely approximated to, being yet quite distinct from them. While this was in the press I detected a precisely similar flap under the distal radii. Again, as touching the notches, these are

[1] The italics are mine.

accounted for by supposing that they are for the purpose of allowing the distal portion of the radius to be turned upon itself without "crumpling." Would it not seem more probable that these notches are—if we are to explain their presence at all—rather to keep the edges of these radii sufficiently far apart to allow not only of the passage of the hooklets, but to prevent their being injured by chafing when in position? The curvature does not seem sufficiently great to account for these notches in the first place; and in the second, seeing that the curve is not delayed till the radius has completed its development, and is then suddenly bent, but that the curvature is synchronous with growth, a far greater inflection could have taken place without any special arrangements, as witness a thousand instances in nature. Lastly, I would point out that the proximal radii, instead of curving abruptly just at the point where the laminæ of the distal radii break up into hooklets, as shown in Wray's figure, are actually not only curved less, but, as already pointed out, extend right across to the next ramus. I have purposely dwelt upon the shortcomings of these figures, because they are rapidly making their appearance into the various text-books. Though this is a fact to be deplored, it may be readily understood. I suppose, nowadays, if one finds himself engaged in bookmaking—of the more honorable kind, I mean—he must add yet more drudgery to his labours by verifying every statement to its minutest details, when probably, by the time he has finished the last chapter, he will have to begin again and bring his work "up to date."

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W. P. Pycraft.

Notes on the Peripatus of Dominica.

By

E. C. Pollard, B.Sc.Lond.

With Plate 17.

A NUMBER of specimens of Peripatus from Dominica, West Indies, have recently been handed over to me for description by Professor Ray Lankester, to whom I owe my best thanks for intrusting me with this material. The specimens were collected by Mr. Ramage in Dominica, and sent, some alive, some preserved in alcohol, to Professor Lankester.

I had, in all, eighty-six individuals, of which fourteen had been opened in salt solution before preserving, whilst the rest were preserved whole.

Size.—There are considerable differences in size; the length, measured without the antennæ, varying from a minimum of 17 mm. to a maximum of 50 mm.

The males are, as a rule, much smaller than the females, and they are also much less numerous. Out of thirty-nine specimens in which I determined the sex only eight are males, and of these the largest is only 25 mm. in length.

On the other hand, a good-sized female measures 42 mm.

There are one or two apparent exceptions to this generalisation, one of the females being only 17 mm. and another only 19 mm. long; but from the fact that I have not found any males longer than 25 mm., and also that the majority of the

females are considerably larger than this, I am inclined to regard the small females as not yet full-grown.

Colour.—My observations as to the colour of this Peripatus have been made entirely upon specimens preserved in spirit.

The general colour of the body is a reddish brown dorsally, with a diffuse longitudinal streak of a darker shade extending down the centre of the back. The median dorsal line is marked by a well-defined narrow band still darker in colour. Ventrally the colouring is much paler, being a light grey or greyish yellow. The colouring of the legs on their dorsal and ventral surfaces corresponds with the colours of the dorsal and ventral body surfaces.

The antennæ are of a dark red-brown shade, with their terminal enlargements much lighter, almost flesh-coloured.

This colouring obtains, with slight individual variations, for all the specimens with one exception. In this unique case the dorsal surface is piebald, with a pale straw-colour and a reddish brown. The brown is disposed as a broad collar, and as two lateral bands just dorsal to the legs; the band on the right side, however, is only present in the posterior region of the body. There is a white median line dorsally. The ventral surface and the legs are pale yellowish white. The antennæ are dark red-brown, with their knobbed terminations pale yellow or whitish.

This specimen is small, and appears to be a young form in which the pigment is as yet not completely developed, or it may possibly be an abnormality.

Ridges and Papillæ of the Skin.—As in the other neotropical species of Peripatus, the ridges of the skin are continued right across the dorsal median line.

The papillæ of the ridges are arranged in a single file of larger ones, or two or three smaller ones occur abreast.

As in P. Edwardsii (Blanchard), there are accessory ridges extending across the dorsal median line, but not reaching far on either side of it; and also, as in P. Edwardsii, the diagonal lines which occur in the Cape species, breaking the surface into lozenge-shaped areas, are absent.

Many of the papillæ, both on the legs and body, are divided into two main portions, a basal and a more distal part. Of these the basal portion is cylindrical in form, thus agreeing with the species from Caracas, and differing from the Demerara species, in which the basal portion of a papilla is conical (fig. 1).

The papillæ vary considerably in shade, some being much lighter than others, and to this is due the speckled appearance of the skin.

Jaws.—Fig. 2 shows that the jaws are very similar to those of P. Edwardsii (4, figs. 25, 26).

The outer blade is provided with a large main tooth, and a smaller but still well-marked secondary one. On the inner blade there is a large main tooth and seven or eight smaller ones, of which the first is closely approximated to the main one, and is considerably larger than the remaining six or seven, from which it is separated by a wide diastema.

Antennæ.—The papillæ on the rings of the antennæ are arranged in several rows.

Ambulatory Appendages.—Only one specimen of Peripatus from Dominica has been previously described, and the authorities differ as to the number of legs possessed by it. Professor Jeffrey Bell states that there are thirty pairs(1), whilst Mr. Sedgwick considers that there are only twenty-nine (4).

In my specimens the number of ambulatory appendages varies from twenty-five to thirty pairs, the great majority having twenty-nine.

The relationship between the number of appendages and the sex of the individual is interesting.

Out of thirty-nine specimens in which the sex was ascertained only eight are males, and each of these is possessed of twenty-five pairs of legs only.

Of the thirty-one females which I have examined, two are possessed of twenty-six pairs of ambulatory appendages, one of twenty-eight, twenty of twenty-nine, and six of thirty; whilst I am uncertain as to the number possessed by the two remaining specimens.

Of the remaining two, one at least possessed more than twenty-seven pairs, but the exact number in both cases is doubtful, since the specimens had been mutilated.

The numbers given above are perhaps better realised when arranged in a tabular form, thus:

8	specimens	with	25	pairs	of	ambulatory appendages.	All males.
2	,,	,,	26	,,	,,	,,	Both females.
1	,,	,,	28	,,	,,	,,	Female.
6	,,	,,	30	,,	,,	,,	All females.
67	,,	,,	29	,,	,,	,,	Of these 20 were opened, and all found to be females.
2	,,	,,	an uncertain number of legs.				Both females.

The male, therefore, seems to be always possessed of twenty-five pairs of ambulatory appendages; whilst the female, with one doubtful exception, has always more than twenty-five pairs.

There are four foot-pads ventrally on each of the ambulatory appendages (fig. 3), with the exception of those of the last pair, which are possessed of two pads only (fig. 4).

At the distal extremity of the foot, close to the claws, there are three primary papillæ, two on the anterior margin of the foot and one on the posterior; but the basal papillæ are absent.

The foot-groove, which in P. capensis extends on to the body surface as far as the median ventral line, is in the Dominican form continued only a very short distance on to the ventral surface.

There are no white papillæ on any of the ambulatory appendages.

In his description of specimens of Peripatus from Guiana and Dominica, Mr. Sclater (3) mentions the occurrence of a "bladder-shaped appendage" attached to the foot-grooves. Such a vesicle-like structure is very obvious on the legs of some of my specimens, but it appears to be due simply to an extroversion of the lining of the groove.

Apertures.—The anus is situated posteriorly between the legs of the last pair.

The generative aperture in both sexes is found ventrally between the legs of the penultimate pair.

The segmental organs of most of the appendages open into the foot-groove close to the junction of the leg with the body. On the fourth and fifth pairs, however, the aperture is situated on a papilla between the proximal and third foot-pads (fig. 5).

Internal Anatomy.—Male Generative Organs (fig. 6). —The vas deferens of each side is extremely short. Each passes under the nerve-cord of its own side, and the two then unite to form a very long coiled ductus ejaculatorius.

A pair of accessory glands are present, but these are much shorter than those of the other South American forms which have been described.

The accessory glands open out independently on either side of the anus, as in P. Edwardsii, not into the ductus ejaculatorius, as described for P. capensis.

In figs. 10 *a*—*c*, three sections through the testis are figured. Of these the most anterior (fig. 10 *a*) is through the prostate (*pr.* in fig. 6), and shows simply a mass of large nuclei surrounded by a single layer of flattened epithelial cells. The layer of epithelium round the nuclei of the prostate is a point to be noticed, since Gaffron (2), in his description of P. Edwardsii, states that there is in this region no epithelial covering to the cells, which are simply enclosed in a thin muscular sac. Gaffron, in fact, makes this a distinction between the prostate (Schlauchhoden) and the testis proper (Blasenhoden). This is well seen in his figure (Taf. xxiii, fig. 46), and is clearly described in his own words :—" Der bedeutsamste Unterschied zwischen Schlauch und Blasenhoden ist jedoch das Vorhandensein eines charakteristichen Epithels im letzterem. Während der dünnhäutige Sack des Schlauchhodens gleichmässig und dicht angefüllt ist mit grossen Zellen, die sich nicht zu einem geschlossenen Wandungsepithel anordnen, liegt der eben beschriebenen Blasenhodenmuscularis innen ein sehr regelmässiges polygonales Pflasterepithel."

It is possible, however, that in P. Edwardsii an epithelial covering to the prostate is also present, but the flattened cells lying close upon the large nuclei below, as seen in fig. 10*a*, may have escaped notice.

The next figure (fig. 10*b*) is from a section through the actual testis (*te.* in fig. 6). The contents of the testis in this region consist of numerous large nuclei and wisps or bundles of spermatozoa. There is a considerable space between these and the epithelium, probably due to shrinkage. The epithelial wall is well seen, and is similar to that described and figured in P. Edwardsii by Gaffron. The cells are higher and the nuclei rounder than in the epithelium of the prostate.

More posteriorly still we get numerous cross-sections of the coiled duct of the testis (fig. 10*c*). The walls of this duct are composed of cells with large round nuclei, and within its cavity are numerous spermatozoa. The whole coiled mass is surrounded by a layer of flat epithelium, and this is continued over the straight portion of the vas deferens, where we have accordingly two layers of epithelial cells,—an inner layer of fairly tall cells with round or oval nuclei, and an outer layer of flattened cells with rod-like nuclei.

In no region of the testis have I found a muscular covering external to the epithelium.

Female Generative Organs (figs. 7—9).—On each oviduct is situated a globular receptaculum seminis (*R. S.*) containing spermatozoa, and possessed of double ducts as in the other neotropical forms. Between the receptacula and the ovary are a pair of sac-like appendages (*R. Ov.*), the so-called receptacula ovorum of Kennel, but I have been unable to make out a vesicle at their distal ends.

Comparison with other Neotropical Species.—The Peripatus of Dominica, P. Dominicæ, resembles the other neotropical species in—

i. The possession of four spinous foot-pads.

ii. The position of the generative aperture between the legs of the penultimate pair.

iii. The division of the primary papillæ into two portions.

iv. The absence of the dorsal white line.

v. The arrangement of the teeth on the inner blade of the jaw, there being a considerable gap between the first minor tooth and the rest.

vi. The presence of the receptacula ovorum and seminis on the oviducts.

vii. The unpaired portion of the vas deferens is of great length and much coiled.

viii. The number of legs is not constant.

Compared with P. Edwardsii, to which the Dominican species is most nearly allied, we find the following special points of agreement:

i. There are two foot-pads only on the legs of the last pair.

ii. The male has a smaller number of legs than the female.

iii. The basal part of the primary papillæ is cylindrical in both.

iv. The jaws and arrangement of the teeth are similar in the two.

v. There is in each a pair of accessory glands opening on each side of the anus.

The chief differences between the two are—

i. The number of ambulatory appendages; of these there are 29 to 34 pairs in P. Edwardsii, and 25 to 30 in P. Dominicæ.

ii. The white tubercles which are present on some of the legs in P. Edwardsii are not found in the species now described.

Compared with P. Trinidadensis.—The Dominican species differs much more from P. Trinidadensis. Besides the difference in the number of ambulatory appendages (P. Trinidadensis having 28—31 pairs), the two forms differ in the number of teeth on the inner blade of the jaw, the Trinidad species having a much larger number than the Dominican. Moreover in the Trinidad Peripatus the basal portion of the primary papillæ is conical, whilst in the Dominican form it is cylindrical.

Compared with P. torquatus.—P. torquatus is possessed of a much larger number of legs than the Dominican form, having 41 or 42. The colouring is also strikingly different, P. torquatus being characterised by a bright yellow band behind the head on the dorsal surface.

Bibliography.

Complete lists of the literature referring to Peripatus have already been published by Mr. Sclater and Mr. Sedgwick, and therefore the following list includes only the papers to which special reference is made in the above description.

1. Bell, F. J.—"Note on a Peripatus from the Island of Dominica, West Indies," 'Ann. Mag. Nat. Hist.,' 5th ser., xi, 1883.

2. Gaffron, E.—"Beiträge zur Anatomie und Histologie von Peripatus," 'Zool. Beiträge' (Schneider), Bd. i, 1885.

3. Sclater, W. L.—"Notes on the Peripatus of British Guiana," 'Proc. Zool. Soc. London,' 1887.

4. Sedgwick, A.—"A Monograph on the Species and Distribution of the Genus Peripatus (Guilding)," 'Quart. Journ. Micr. Sci.,' New Ser., xxviii, 1888.

EXPLANATION OF PLATE 17,

Illustrating Miss E. C. Pollard's paper, "Notes on the Peripatus of Dominica."

Fig. 1.—Primary papilla from skin of Peripatus.

Fig. 2.—Inner and outer blades of jaw.

Fig. 3.—Leg of Peripatus, showing four foot-pads.

Fig. 4.—Last leg of specimen with twenty-nine pairs, possessed of two foot-pads only.

Fig. 5.—Fourth leg, showing aperture of nephridium between the third and proximal pads.

Fig. 6.—Male generative organs. *Ac. gl.* Accessory gland. *D. Ejac.* Ductus ejaculatorius. *N. C.* Nerve-cord. *Pr.* Prostate. *Te.* Testis.

Fig. 7.—Female generative organs. *Lig.* Ligament of attachment. *N. C.* Nerve-cord. *Ov.* Ovary. *R. S.* Receptaculum seminis. *R. Ov.* Receptaculum ovorum. *Ut.* Uterus.

Fig. 8.—Enlarged view of ovary and receptacula. Reference letters as in Fig. 7.

Fig. 9.—Diagram of the same.

Fig. 10.—Transverse sections through the testis.

10*a*.—Through the prostate.

10*b*.—Through the testis proper.

10*c*.—Through the coiled duct of the testis. *Ep.* Epithelium.

Outlines drawn with Zeiss, oc. 4, obj. B; and details filled in with Zeiss, oc. 2, obj. D.

Fig. 11.—Transverse section through vas deferens.

Fig. 1.

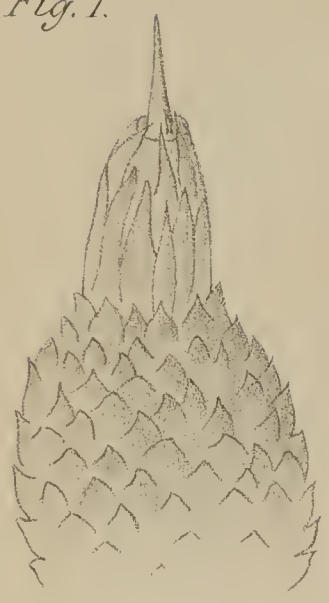
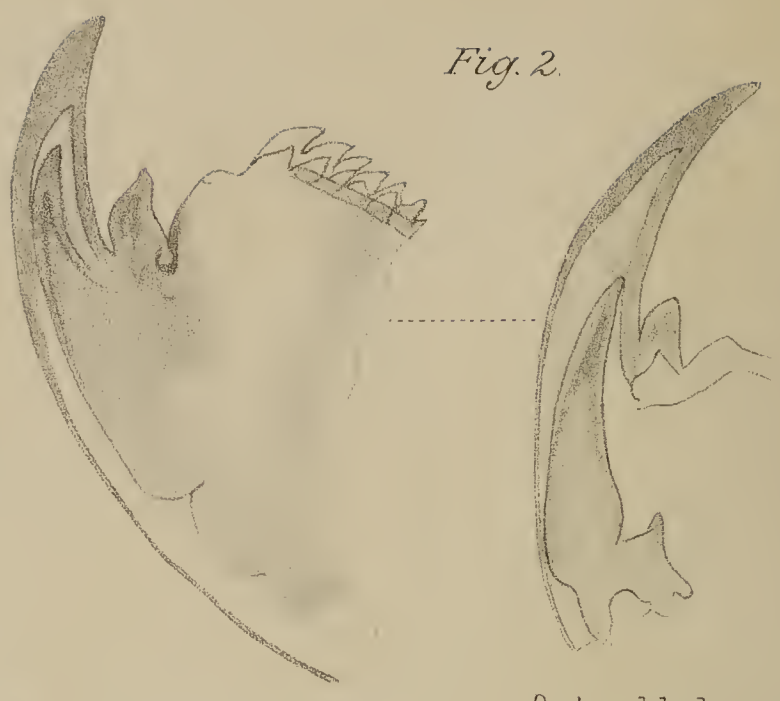


Fig. 2.



Inner blade.

Outer blade.

Fig. 3.

Fig. 6.

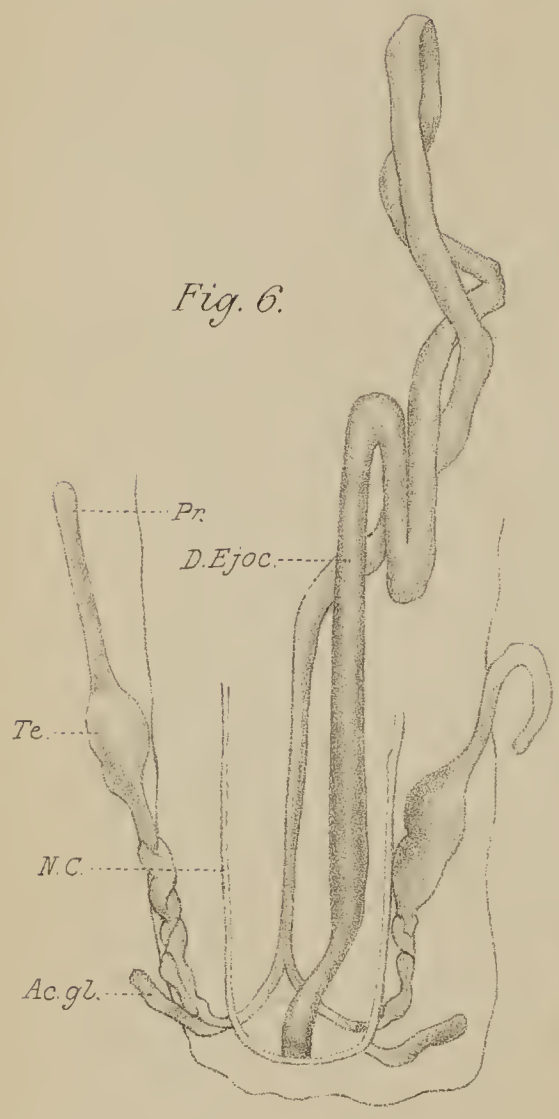


Fig. 7.

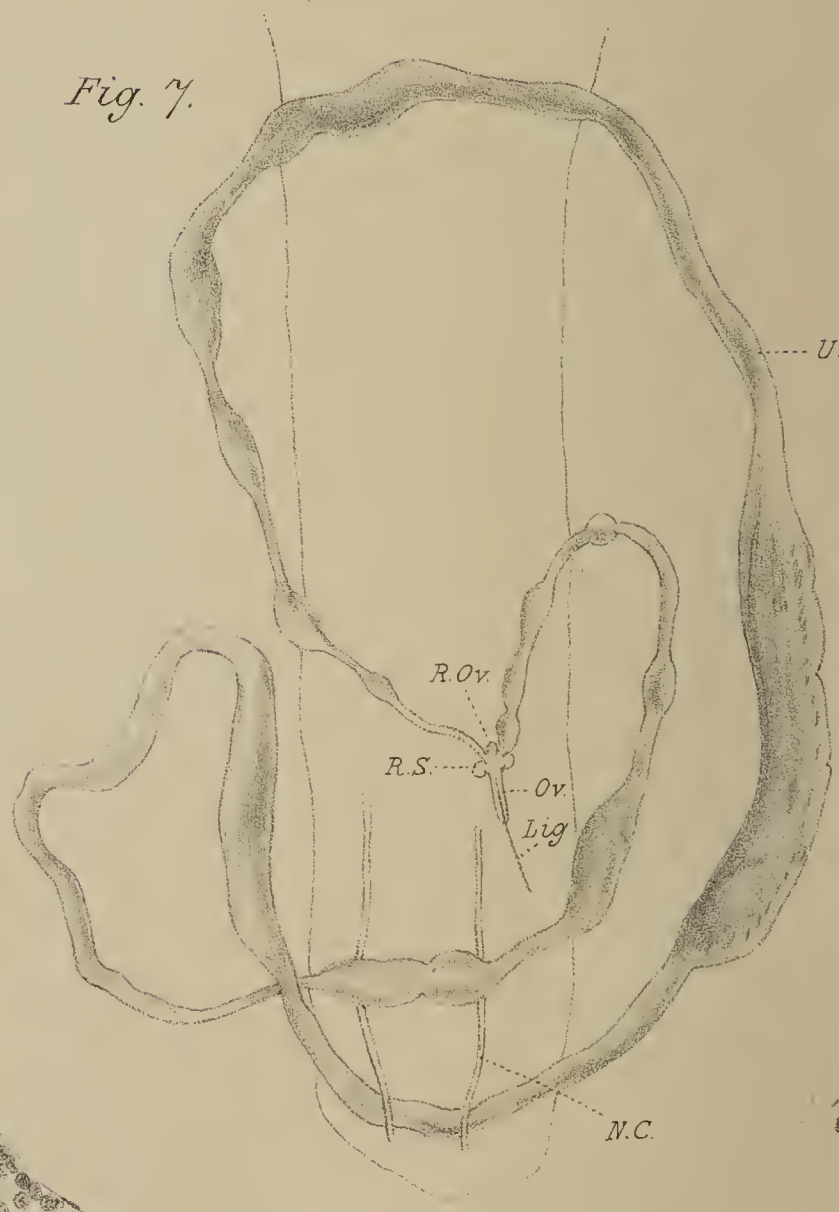
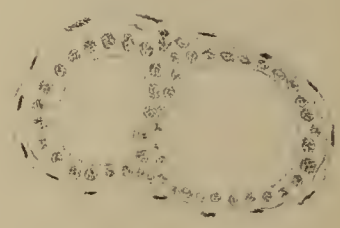


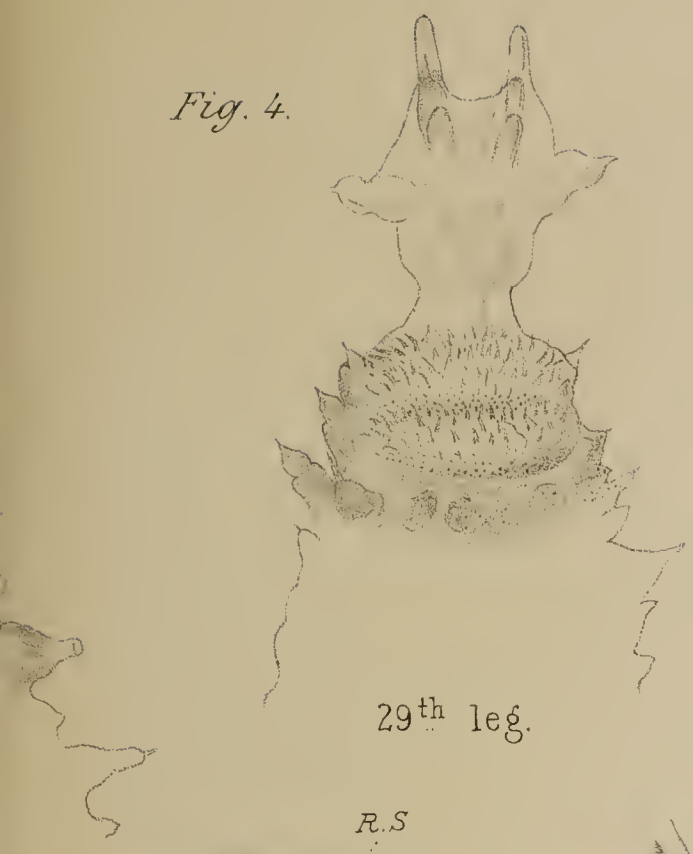
Fig. 10.a

Fig. 11.



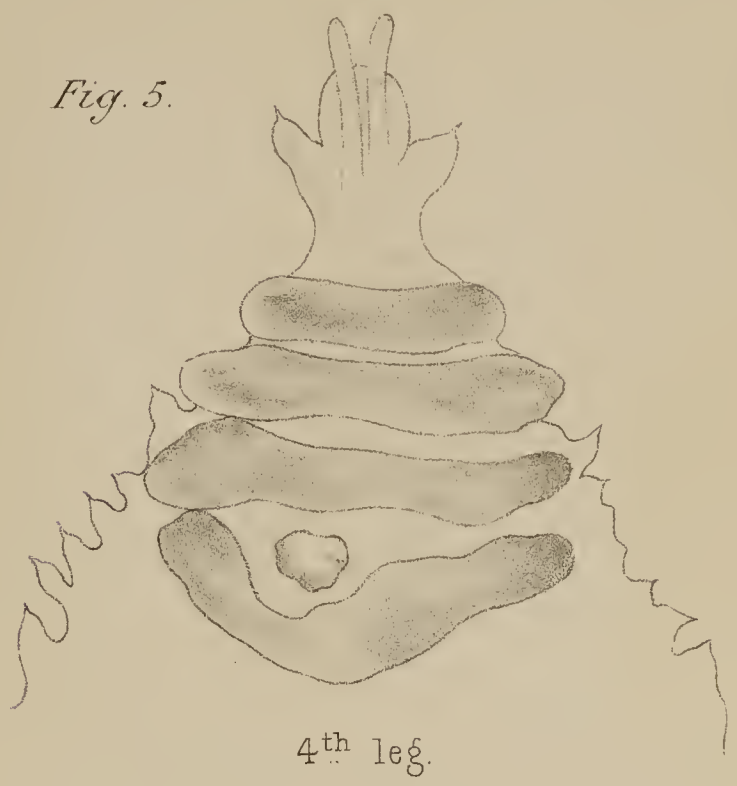
E.C. Pollard del

Fig. 4.



29th leg.

Fig. 5.



4th leg.

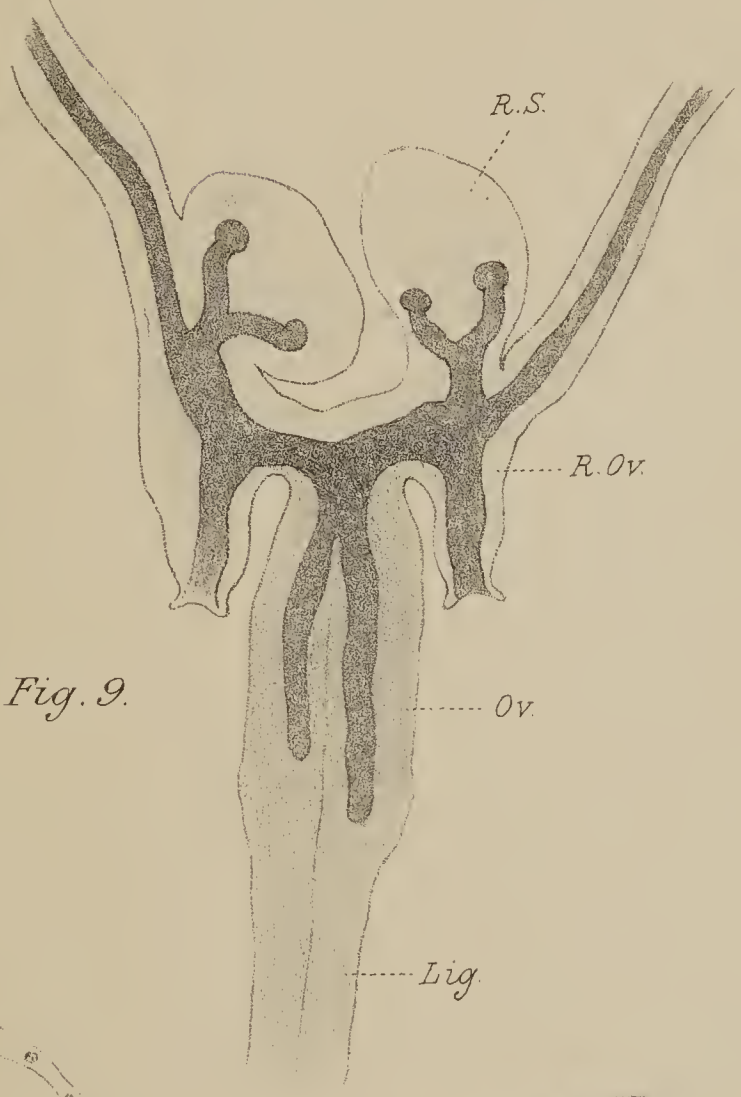


Fig. 9.

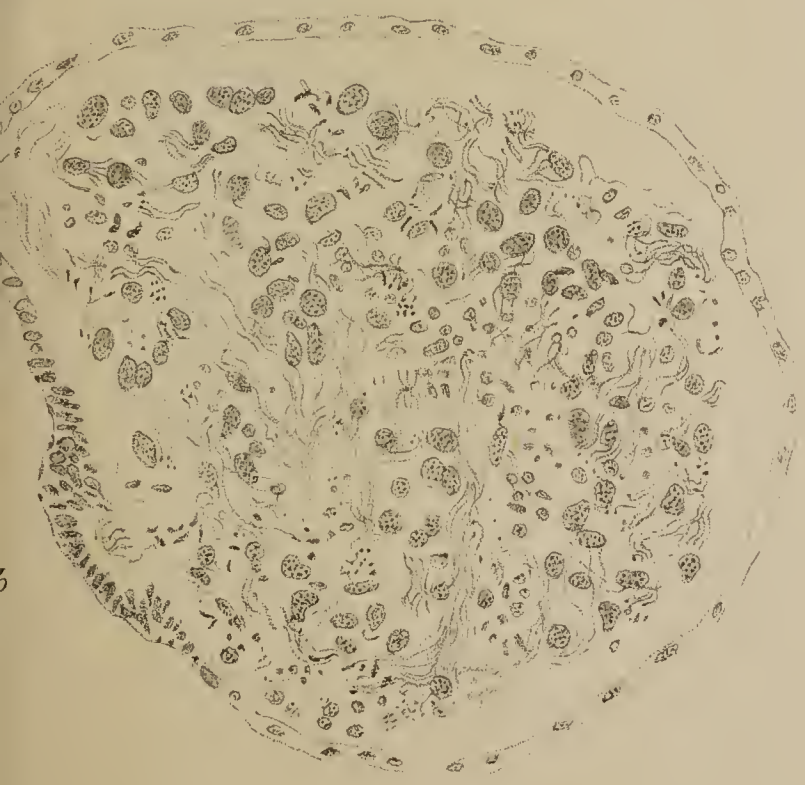
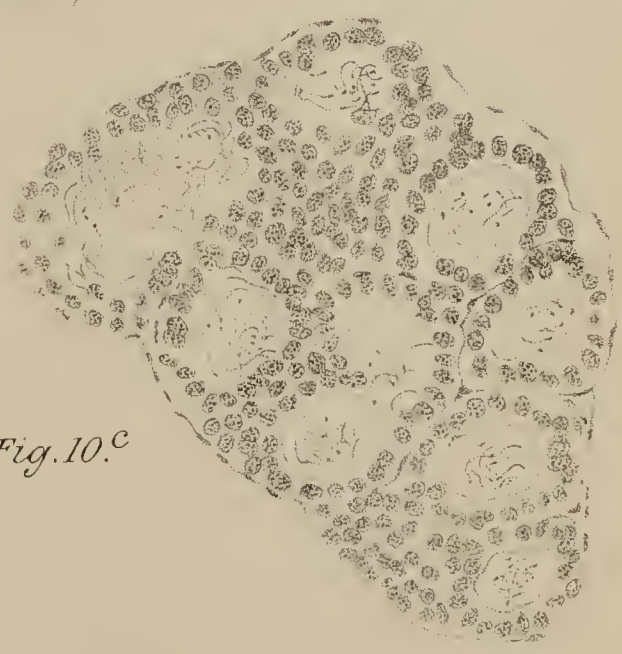


Fig. 10.c



F Huth, Lith.r Edin.r

On the Fossil Mammalia from the Stonesfield Slate.

By

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With Plate 26.

Ever since the discovery, made some eighty years ago, of Mammalian remains in the Stonesfield Slate near Oxford, these fossils have excited the interest of naturalists, and have been the subject of much discussion amongst geologists and palæontologists both in England and abroad. Nevertheless something still remains to be described in the few specimens which exist; and, while one of them has not yet been figured at all, others have been only inaccurately represented. I therefore propose to write a short history of each fossil, as far as it is known, giving figures when necessary; and to sum up the most important results which have been reached with regard to them by previous authors, together with some remarks as to the bearing of the facts ascertained by a careful study of the teeth belonging to these remains on the general question of the origin and homology of the cusps of Mammalian teeth.

Besides the fragment of the multituberculate form Stereognathus, which I shall mention later, there are only twelve undoubted fossil Mammalian remains from the Stonesfield Slate at present known; ten of these are lower jaws, two are limb bones. Six of the fossil jaws are in the Oxford Museum, one in the York Museum, one in the private collection of

Mr. Parker of Oxford;[1] the two remaining jaws and the limb bones are in the British Museum.

Through the kindness of Professor Green and of Professor Lankester, who placed the Oxford fossils in my hands for the purpose of displaying them in a museum case in a manner more worthy of their interest and value, I have had the opportunity of examining and handling our six specimens. I am much indebted to Dr. Henry Woodward for allowing me to examine the two British Museum fossils, and to Mr. Parker for lending me his. To the authorities of the Museum at York I must express my thanks for lending me the excellent specimen in their keeping; but more especially to Professor Lankester, who spared himself no trouble in obtaining for me this privilege, and who has further given me much help during my researches.

It may here be mentioned that I have been able, by carefully working away the matrix with sharp needles under Zeiss's dissecting microscope, to expose new cusps, and in some cases new teeth, in five of the jaws described. My figures, which I have endeavoured to make as faithful as possible, differ, therefore, considerably from those previously published.

The formation from which these fossils were obtained belongs to the Lower Jurassic period; whence the great interest attached to them, for at the time of their discovery they were by far the earliest known remains of warm-blooded Vertebrates, —being, in fact, the first Mesozoic Mammalia obtained. Since then, as is well known, remains of a few fossil Mammalia have been found both in England and elsewhere in strata belonging to the Triassic age; as, for instance, Microlestes in England, Dromatherium in America, and Tritylodon in South Africa.

The two fossil limb bones mentioned above have been figured and described by Professor H. G. Seeley (29). As, unfortunately, they afford no clue to the relationship of the animals whose jaws are described below, there being no proof

[1] Mr. Parker also has in his possession a toothless fragment of a jaw which may perhaps be Mammalian.

that these bones belonged to any of them, I need only mention that Seeley considers that they are "limb bones indicating a generalised insectivorous type, modified from a Monotreme stock in the direction of the Marsupial plan."

Genus Amphitherium.

Four of the fossil jaws appear to belong to this genus. Three of these, two of which are type specimens, are in the Oxford Museum; the fourth is in the British Museum.

Amphitherium Prevostii, Blainville.

Type specimen, Pl. 26, fig. 1.

A left ramus of the lower jaw, seen from the inside; in the Oxford Museum.

In 1824[1] Dr. W. Buckland, the well-known geologist, first announced the discovery of the remains of mesozoic Mammalia in his paper 'on Megalosaurus' (5). He there mentions "two portions of the jaw of the didelphys or opossum," which he refers "to this family on the authority of M. Cuvier, who has examined it." From Mr. W. J. Broderip we learn that these rare fossils were obtained as follows:—"An ancient stonemason living at Heddington . . . made his appearance in my rooms at Oxford with two specimens of the lower jaws of mammiferous animals, embedded in Stonesfield slate. . . . One of the jaws was purchased by my friend Professor Buckland, who exclaimed against my retaining both" (4). The fossil purchased by Broderip himself is the type specimen of Phascolotherium (see below); Buckland's fossil is the type specimen with which we are now concerned. He placed it in the Ashmolean Museum, whence it has come with the other specimens of the Buckland collection to its present home, the Oxford University Museum. The exact date at which it was purchased I have been unable to ascertain for certain; it was probably about 1814: the date given by Zittel is 1812 (32), but I know not on what authority.

Cuvier, who visited Oxford in 1818, says of these fossils

[1] Not 1823, as is generally stated to be the case.

that "lors d'une inspection rapide que j'en pris à Oxford, en 1818, [ils] me semblèrent de quelque Didelphe;" and adds in a note that the jaw of Amphitherium "est celle d'un petit carnassier dont les machelières resemblent beaucoup à celles des Sarigues, mais il y a dix dents en série, nombre que ne montre aucun carnassier connu" (8). This note was written after the examination of some careful drawings of Buckland's fossil and of the type specimen of Amphilestes (see below) sent to him by Prévost, who was then travelling in England.

These announcements of the discovery of Mammalian remains in stone belonging to the Mesozoic age created a great sensation amongst the palæontologists of the time, and it was not for more than twenty years afterwards that the opinion of the great French naturalist was generally accepted. Some contended that the fossil did not really belong to the slate, others that the strata in which they were found were not of the Mesozoic period; while others, again, urged that the jaws were those of a reptile, or even of a fish. All doubt having been set at rest with regard to these points, it will not be necessary to enter here in detail into the arguments used on either side.

Prévost, in 1825, on his return from England, where he had carefully examined the specimen of Amphilestes now at York, and "le fameux Didelphe" in Buckland's collection, published the first detailed description and figure of this the type specimen of Amphitherium (25). He describes the teeth as having tricuspid crowns, and two distinct roots in alveoli, concluding that the fossil was Mammalian in confirmation of Cuvier. As to its relationship, Prévost considered that it was probably "un mammifère carnassier insectivore qui pouvait offrir quelque analogie avec les Didelphes, mais qui appartiendrait à un genre inconnu."

Agassiz, in 1835, mentions the Stonesfield fossils in a short note (1). He considered that the remains were not sufficient to allow of a certain determination of their affinities, but drew attention to the resemblance of the teeth (especially those of Phascolotherium described below) to those of certain

seals possessing tricuspid molars. Owen mentions (20) that Agassiz proposed the name Amphigonus for Amphitherium, in the German translation of Buckland's Bridgewater Treatise (which I have not seen).

Dr. Buckland, in 1836, gave a rough figure of this jaw, together with enlarged drawings of two of the teeth (6).

Two years later M. de Blainville published his "Doutes sur le prétendu Didelphe de Stonesfield" (2), in which he tried to prove that the fossil in question, of which he reproduced Buckland's figure, belonged to a reptile. In this paper he laid considerable stress on the fact that "une portion de mâchoire inférieure, rapportée de Stonesfield par M. Brochant de Villiers et ses élèves MM. Elie de Beaumont et Dufrénoy, et qu'on avait supposée appartenir au même Didelphe," had been proved to be reptilian, and accepted as such even by Cuvier. Blainville mistook the mylohyoid groove,[1] well marked in our specimen, for a suture indicating that the jaw was of a compound structure: a similar mistake was made in the case of the other jaws. He proposed the generic name Amphitherium, which has since been generally adopted.

Buckland then took with him to Paris the type specimen of Amphitherium and the second fossil of the same species now in the Oxford Museum, which will be described below. He showed these to M. Valenciennes, who made a careful study of them, publishing a detailed account mainly confirming the results of Cuvier and Prévost, in which the name Thylacotherium Prévostii is proposed (31). Unfortunately Blainville was not convinced, as he did not see the fossils, for he tells us that "le jour où M. le docteur Roberton voulut bien m'inviter à passer la soirée chez lui avec M. Buckland, je partais pour la campagne" (3). He therefore only brought forward "Nouveaux doutes" (3), in which we learn that "M. Buckland lui-même a exposé le problème et les pièces sur lesquelles il repose à l'investigation des naturalistes allemands reunis en congrès à Fribourg, en Brisgaw, au mois de septembre dernier" (1838). In his contention as to the saurian

[1] For a full discussion of the mylohyoid groove see Osborn (14).

character of these remains, Blainville was opposed in Paris by Duméril (9) and Geoffroy Saint-Hilaire (27), whilst in England he was supported by Professor Grant (11) and by Ogilby. The latter took up a more impartial position, and considered that they were not justified by the evidence in pronouncing whether the fossils were mammalian or reptilian, arguing in favour of saurian affinities that the molars and premolars could not be distinguished, that the canine and incisors occupy five twelfths of the dental line, that the incisors (in the type Phascolotherium) are nearly in the same straight line as the grinders, and that the condyle is below the level of the crown of the teeth (13).

On returning to England, Buckland entrusted to Owen these "bones of contention," as the latter calls them, for the purpose of making an exhaustive study to ascertain their true nature. In 1838 Owen read two papers on this subject before the Geological Society (18), and in 1842 his full treatise was published with carefully executed figures (19). Owen drew attention to such Mammalian characters as the convex articular condyle, the broad, high, and curved coronoid process, situated immediately in front of the condyle and resembling that of the opossum, and the separate angle inflected as in Marsupials and some Insectivora. He then described the teeth in detail, comparing the six molars of Amphitherium to those of Didelphys, and the four premolars to those of Didelphys and Talpa. For the first time Owen definitely pointed out that the molars of these animals closely resemble each other, belonging to the type of tooth now known as the tritubercular-sectorial. "An interesting result of this examination is the observation that the five cusps of the tuberculate molares [of Amphitherium] are not arranged, as had been supposed, in the same line, but in two pairs placed transversely to the axis of the jaw, with the fifth cusp anterior, exactly as in Didelphys, and totally different from the structure of the molares in any of the Phocæ, to which these very small Mammalia have been compared" (18). It is surprising, after this, to see Professor Osborn, fifty years later, claiming the "discovery" of tritubercular molars in Amphitherium (15).

In subsequent works Owen again describes and figures this jaw (**20, 21, 23**); a "diagram" of it is given by Professor Phillips in his 'Geology of Oxford' (**24**).

In 1888 Professor H. F. Osborn published his interesting memoir on the 'Mesozoic Mammalia of the Old and New Worlds,' in which he treats of the Amphitherium jaws (**14**). Unfortunately the description of the molars is quite erroneous, owing to the author's considering that the cusps were all in the same line. "The fact is," says Osborn, "these crowns of the molars consist of an elevated anterior and median cusps, followed by a low posterior heel, and with an internal cingulum rising into the low cusp on the inner face of the median cusp." At this time Osborn had only seen drawings and published figures of the Oxford jaws, but shortly after, during a second visit to England, he examined them himself, and corrected his mistake in a subsequent publication (**15**), finding the external cusp described half a century before by Owen.

I have nothing to add to these descriptions, excepting the fact that Owen was wrong in considering the median projections in molars 4 and 5 as being the external cusp (which he found in molars 2 and 6); they are simply the surface where the internal cusp has been broken off, and I have exposed in these two teeth the external cusp itself, which was previously hidden (see figure).

The second specimen in the Oxford Museum (Pl. 26, fig. 2) is a left ramus, seen from the inside.

Valenciennes was, I believe, the first to mention this fossil (**31**), which was one of the two brought over to Paris by Buckland in 1838. The French author, however, erroneously considered it was "de la même espèce que celle décrite et figurée par M. Broderip, son Didelphys Bucklandi" (Phascolotherium).

Owen figured and described it correctly (**19—21, 23**) as a left ramus containing one molar behind, separated (by a gap wide enough to allow for four molars) from two entire and two

broken premolars.[1] In front of these Owen detected the sockets for six teeth.

Osborn has lately (15) discovered a young molar emerging from the jaw just behind and within the posterior molar.

The British Museum specimen (Pl. 26, fig. 4) is a portion of the right ramus, inner view.

This fossil has been partially figured by Osborn in his first treatise (14), who took it to belong to a left ramus; but in his later paper (15) he recognised its true character by the presence of the "double internal cusps [of the molars], by the cingulum upon the premolar, and by the faint mylohyoid groove near the lower border," adding in a note that "it would be well to run the risk of injuring one of these molars to expose the external cone."

The jaw, which is figured here complete and in detail for the first time, although much broken is really the most instructive of the four specimens extant of this genus, as regards the structure of the molars. In front are the traces of four teeth, followed by an entire premolar. The latter possesses a laterally compressed crown bearing one large cusp, a very small anterior cingulum cusp, and a posterior heel. On the whole this tooth is very similar to the premolars of the other Amphitherium jaws. The molars, of which there are five remaining, when I first examined them displayed only the two nearly equal and pointed cusps of the inner margin, and a simple low posterior heel (as shown in the figure by the third and fourth molars); by carefully clearing off the matrix I have exposed the large external cusp (protocone) in the first, second, and fifth molars (see woodcuts, figs. 1 and 2). In the latter tooth I have also exposed the full extent of the posterior heel, which is seen to rise on the external margin into a pronounced cusp; the internal cusp is hardly distinguishable from the general margin of the heel at its postero-internal angle. The heel is somewhat narrower than the body of the tooth at the

[1] The posterior premolar bears a small internal cusp (= the deuterocone of Scott ?).

level of the more anterior external cone, and a "basin," if it can be said to exist at all, is small and shallow as far as I have been able to ascertain.[1] It should be noticed that this

Fig. 1

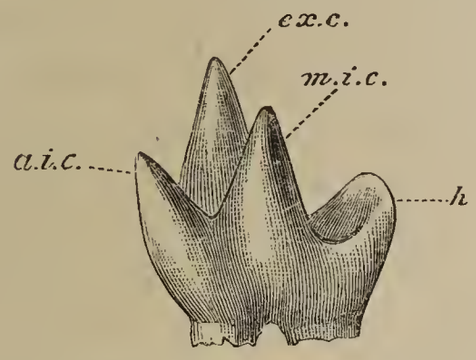

Fig. 2.

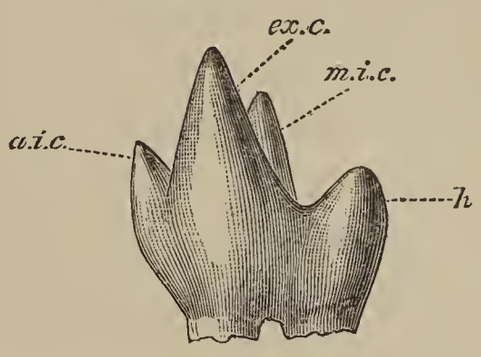

Fig. 1.—Inner face of a molar of the right ramus of the lower jaw of Amphitherium Prevostii.

Fig. 2.—Hypothetical representation of the outer face of the corresponding molar of the left ramus. *a. i. c.* Anterior internal cusp (paracone). *ex. c.* External cusp (protocone). *h.* Heel. *m. i. c.* Median internal cusp (metacone).

The teeth are represented as if entirely freed from the matrix.

is the first complete tooth of the tritubercular-sectorial type which has been seen in the Stonesfield fossils.

Amphitherium Oweni, Osborn.

The type specimen in the Oxford Museum; a right ramus with the external surface exposed (Pl. 26, fig. 3).

The type and only specimen of this species, obtained with the other jaws from Dr. Buckland's collection, was found probably about 1845. It was first described and figured by Owen in his 'History of British Fossil Mammalia' in 1846 (**20**), and subsequently in his Monograph (**23**) and Odontography (**21**) under the name of A. Prevostii. This specimen, perhaps the most perfect of all the Stonesfield jaws, shows very clearly the angle which, according to Owen, exhibits a degree of inflection which is "less than in any of the known Marsupialia, and does not exceed that of the Mole or Hedgehog" (**20**). He describes the six posterior molars as quinquecuspidate, but

[1] Judging from other jaws, we may presume that the heel is, if anything, better developed in the anterior molars.

these teeth are (at all events at the present time) so mutilated that it is scarcely possible even to recognise their tritubercular character. The outer cusps have been entirely broken away, and only traces of the two inner cusps and the posterior heel remain.

An outline figure of this fossil has been given by Phillips (24). Professor Osborn in his first paper (14) separated this specimen from the genus Amphitherium with the name of Amphitylus Oweni, under the impression that the molars were tricuspidate.[1] There can now be no doubt that this view is erroneous, and that the teeth are really, as Owen described them, of the Amphitherium pattern. Zittel (32) follows the latter in including it in the species A. Prevostii; but I have retained it as a separate species, chiefly on account of some considerable differences exhibited between the shape of the jaw of this fossil and that of the specimens described above. The coronoid process is straight above and more pointed at its posterior extremity; the condyle is more slender, the notch between it and the coronoid process being more pronounced; the angle is rather larger, and produced farther back. The premolars, as exemplified by the third and only entire one in this jaw, differ somewhat from those of A. Prevostii; the cusps are more rounded, the main cusp is situated not near the centre of the tooth, but well forward, and the swelling on the fangs, also rather large in the molars, is strongly developed. The molars are unfortunately too broken to compare in detail with those of the previous species.

The question of the lower dental formula of this genus has been purposely left until after the description of all the specimens. Owen, who evidently saw the second Oxford Amphitherium (Pl. 26, fig. 2) in a more perfect condition than that in which it now is, gave the formula i. 3, c. 1, pm. 6, m. 6 (19), describing eight sockets in front of the anterior broken premolar. There can be little doubt, however, that he overestimated the number of teeth anterior to the four premolars. In front of these can still be seen the broken roots of what was

[1] Osborn has since changed his mind, and now, I believe, includes this specimen in the genus Amphitherium.

probably a small premolar, and the next two sockets are most likely those of a double-fanged canine, such as we find in many other mesozoic Mammalia. Four incisors account for the anterior sockets. On the other hand, the type specimen (Pl. 26, fig. 1) has six molars, and four molars beyond which the jaw is broken; so that on combining the two we get the formula i. 4, c. 1, pm. 5, m. 6.[1] The dentition of A. Oweni conforms perfectly to this; we find four incisors, a double-fanged canine, followed by eleven teeth, of which five were probably premolars and six molars. This is also the conclusion reached by Osborn (15) for the dental formula of Amphitherium.

Genus Phascolotherium.

There are three jaws belonging to this genus—the type specimen in the British Museum, a specimen in the Oxford Museum, and one in Mr. Parker's collection. They are all placed in one species.

Phascolotherium Bucklandi, Broderip.

The type specimen, a right ramus with the inner surface exposed, in the British Museum.

This is the fossil mentioned above as having been obtained by Mr. Broderip, together with the type specimen of Amphitherium, about 1814. It must, therefore, be the other of the "two portions of the jaw of the Didelphys" which Buckland tells us were seen by Cuvier (5). This jaw was lost for a time, but, on being found again, was described and figured by Broderip in the 'Zoological Journal' of 1828 (4). He there described the teeth as consisting of seven grinders, one canine, three incisors, and the alveolus of a fourth, naming the jaw Didelphys Bucklandi.

It has been figured by Buckland (6), by Blainville (2), by Owen (19—21, 23), and lastly by Osborn (14).

[1] The second Oxford specimen is the only jaw which shows definite signs of having had five premolars; A. Oweni affords no certain evidence in this respect.

In his writings on this jaw Owen describes the rounded and sweeping outline of the lower margin, the wide recurved coronoid process resembling that of the "zoophagous Marsupials," the notch between the coronoid process and the condyle being especially like that in Thylacinus. Other resemblances he also finds to Thylacinus, namely, in the inflected angle and the molars, whilst the condyle is said to be more like that of Dasyurus and Didelphys. A well-marked mylohyoid groove is present, and the dental foramen is far forward, as in other related Mesozoic mammals. Owen claims that the "molars" (grinders or cheek-teeth) of Phascolotherium resemble those of Thylacinus in number (seven in both cases) and in shape, both possessing three main cusps in a line and two accessory fore-and-aft cingulum cusps, very small in the case of the living Marsupial. He could distinguish no difference between premolars and molars, and looked upon the grinding teeth as being in a simple condition in which the two varieties were not differentiated.

All observers have noticed the peculiar pitting of the surface of the grinders of Phascolotherium.[1] Osborn, in his first paper, also held the view that the seven grinders could not be distinguished into premolars and molars: "A close study of m. 1 shows that it possesses in miniature the characteristic features of the other molars, three cusps and a basal cingulum" (14). In the 'Additional Observations' (15), after examining all the specimens of this species, he writes, "The *first* tooth behind the canine has a main cusp like that of the posterior molars, and an internal cingulum horizontal and rising in two points, instead of showing the sweep downwards and backwards which is so characteristic of premolar cingula. The accessory cusps are either covered with matrix or broken off. . . . . The chief interest lies in the main cusp [of the second tooth], which is loftier and more pointed than the protocone

[1] It is interesting to notice that the teeth of Phoca barbata, which resemble them so closely in shape (as pointed out by Agassiz, 1), also exhibit a pitting of the surface, which might lead one to believe that they are both adapted to some similar kind of food.

of the *third* tooth, which in turn has all the characteristics of a molar." Osborn concludes that the formula may be provisionally written i. 4, c. 1, pm. 2, m. 5. In assigning this formula to Phascolotherium I entirely agree with Professor Osborn, and can only say that the difference between the first two grinders and the succeeding molars is perhaps even more marked than he has described.

The Oxford Museum specimen; a left ramus, seen from the inside (Pl. 26, fig. 8).

This specimen has been figured in outline by Phillips (24) and mentioned by Osborn (15). Mr. Lyddeker, in the British Museum catalogue (12), erroneously referred it to the genus Amphilestes.

Behind are four molars in very good preservation, showing the marked cingulum rising in the two internal points characteristic of the genus; in front and behind the cingulum forms small, sharp cusps. I have lately exposed from the matrix an entire incisor, and as far as possible the sockets of the other teeth which are missing. This jaw is, therefore, now of some use in making out the dental formula. Posteriorly we have the four molars already mentioned, and immediately in front of these are two sockets, presumably belonging to the first molar. Then come two pairs of sockets, of which the anterior is much the smallest, in which were the two premolars. In front of these, again, is the large alveolus of the canine, preceded by two sockets for two incisors. Next comes the incisor recently brought to light, which in shape is stouter at the base, more closely resembling the incisors of Thylacinus than seem to do those of the type specimen. Beyond this tooth the jaw is slightly damaged; the first incisor has probably been broken away. The dental formula of this jaw would then agree with that given by Osborn for the type specimen, and adopted here.

Mr. Parker's specimen; a portion of the right ramus with the inner surface exposed (Pl. 26, fig. 9).

This, the third and last specimen of Phascolotherium, is the

hinder portion only of the ramus, with three molars in situ. It has been figured in outline by Phillips (24), and mentioned by Osborn (15). As the latter notes, it is remarkable for the great development of the coronoid process. The articular condyle is slender and very well preserved; and the broken angle, which I have recently cleared from the matrix, can be clearly discerned. From the fractured surface we may conclude that the angle was very much inflected, and exceedingly thin and flat near its point of attachment; unlike the same process in living Marsupials, it was situated entirely behind the dental foramen. In front of the teeth are the impressions in the matrix of the two anterior molars.

Genus Amphilestes.

Of this genus there are three specimens, included in one species, two of which are in the Oxford Museum, and one in the museum of the Philosophical Institution at York.

Amphilestes Broderipii, Owen.

The type specimen in the museum at York; a left ramus with the inner surface exposed (Pl. 26, fig. 5).

Valenciennes was the first to mention this fossil in 1838. He says, "Une autre mâchoire, que je crois être de cette dernière espèce [Phascolotherium Bucklandi], fait partie du cabinet de M. Sykes" (31). The Rev. H. Sykes presented it to the museum in which it now rests. Valenciennes, "d'après le dessin qui a été envoyé par M. Phillips à M. Cuvier," mistook it for a right ramus seen from the outside. Owen, in the same year, described it briefly under the name of Amphitherium Broderipii,[1] giving an elaborate but in some respects erroneous and misleading figure (19), which has since been frequently copied in his own and other writers' works (20—23). In this, and in all his subsequent figures, Owen represents the angle of the jaw as separate and hardly inflected (as in Amphitherium), and the coronoid pro-

[1] Owen remarks that it appears to be closely allied to Phascolotherium.

cess as angular and small. Phillips (24) and Osborn (14) followed him in this; but in his second paper Osborn recognised the fact that the angle is "precisely as in Phascolotherium" (15),—that is to say, it is inflected and confluent with the condyle.

Owen described the molars with their three high-pointed cusps in a line (much more pointed than those of Phascolotherium), their well-developed internal cingulum rising in two fore-and-aft cusps, and one internal median cingulum cusp. The premolars have no cingulum, and possess one main median cusp with a small cusp in front and behind. There are five molars in situ behind, separated by a gap for one tooth from three premolars; in front of these all the teeth are missing except one incisor, which I have exposed from the matrix.

The jaw is much damaged posteriorly, but the impression of the condyle and coronoid process is still visible in the matrix. The process is seen to resemble in shape that of Phascolotherium, although it is relatively smaller.

The first specimen in the Oxford Museum; a left ramus with its outer surface exposed, reversed (Pl. 26, fig. 6).

Professor Phillips first figured this jaw in outline in his 'Geology of Oxford' (24), probably soon after its discovery. By mistake he put one more molar in the figure than the number exposed in the fossil.[1] Osborn also mentions this specimen (15).

The coronoid process, condyle, and angle are unfortunately broken. I have exposed an entire fifth molar behind the four molars previously visible, the broken base of an anterior incisor, and have rendered what remains of the other incisors more distinct. The molars have no cingulum on the outer surface, but the sharp lateral cingulum cusps are well seen, especially the hinder one.

The second specimen in the Oxford Museum; a portion of the right ramus seen from the outside (Pl. 26, fig. 7).

[1] Apparently this eminent and keen-sighted geologist "could see through a stone wall" better than most people, for the fifth molar which he thus figured has now been brought to light, twenty-two years after (see figure here given).

This fossil has never been figured before; it was probably obtained about 1875. The coronoid process and the condyle have been broken; there are eight consecutive teeth present—five molars and three premolars. These teeth resemble in every particular those of the foregoing specimen.

The dental formula of this genus has hitherto been very difficult to settle, but the working out of the new teeth and of the sockets of the missing teeth has rendered the task easier.

Owen, who only studied the York specimen, assigned to it the formula i. 3, c. 1, pm. 6, m. 6 (23). He considered that the tooth missing between the molars and premolars had been a molar. In front he made out sockets for the three additional premolars, the canine, and the incisors. However, these so-called sockets were mere undulations of the edge of the matrix, not corresponding to the true sockets which I have now exposed. Mr. Lyddeker (12) gives the probable formula as i. 4, c. 1, pm. 4, m. 7, which was adopted by Osborn in his first paper (14). After personally examining the three specimens Osborn gives the formula "with considerable certainty as follows:—i. ? 3, c. 1, pm. 4, m. 6" (15). He tells us that "the Oxford specimens show that there were but *six* molars instead of seven. . . . . In fact, one . . . . specimen . . . . shows but five molars. If this specimen be adult, as seems improbable, it may represent a new genus transitional between Amphilestes with six molars and Triconodon with four" (15). I must confess that I am quite unable to see how one specimen with five molars and another with four (at that time) can even without "certainty" lead to the adoption of the formula m. 6. The ingenious speculation as to the intermediate genus seems to be quite unnecessary when we now know that all the existing specimens possess five molars, and show no signs of having had more or fewer. The premolars are more difficult to deal with. If we measure the distance between the last molar[1] and the first premolar in the first and second Oxford specimens we find that the eight consecutive teeth occupy exactly the same space

[1] In these measurements I have found it convenient to measure from the middle of one tooth to the middle of another.

(10 mm.) in both cases. Measuring now the space occupied by the eight posterior teeth in the York specimen (including the gap as one tooth), we find that it is the same as in the others. There can, therefore, be little doubt that the missing tooth was a premolar, the fourth. Returning to the first Oxford specimen—in front of the three premolars is a space with two sockets, which were evidently occupied by the first premolar, still present in the York jaw. In front of the first premolar we have a region which must be carefully compared in both fossils. As this region in the York specimen is broad and flat, and cannot well be seen from the side, I have given a figure of it more from above (Pl. 26, fig. 5 *a*). The new and only incisor present appears to be the fourth, and three sockets are visible in front of it. Between the incisor and the first premolar are two large sockets, somewhat difficult to account for. If the first of these represents a missing canine, and the second a small premolar, we would have one more post-canine tooth in this jaw than in the Oxford specimen (see above). On the other hand, if they both belong to a large double-fanged canine,[1] we would then apparently have only three incisors in the Oxford jaw, assuming that here also the canine occupied two sockets.[2] On examining the latter specimen closely it is seen that the anterior extremity of the jaw is broken; moreover the distance from the extremity to the second premolar in the York Amphilestes is 2 mm. longer than in the Oxford specimen. There is, then, no great difficulty in supposing that in the latter the first incisor has been broken away.

Provisionally the formula of Amphilestes Broderipii may therefore be written i. 4, c. 1, pm. 4, m. 5.

As for the systematic position of these Stonesfield fossils, the remains are too scanty to allow us to form any very definite opinion. Owen considered Phascolotherium to be

[1] Double-fanged canines are not uncommon amongst Mesozoic Mammalia.

[2] It is to be noticed that in both the jaws these sockets touch one another, whilst there is a small space on either side of them. Should the York fossil prove to have possessed ten teeth behind a single-fanged canine, it would have to be separated from the Oxford specimens.

marsupial and nearly related to Thylacinus; Amphitherium, on the other hand, he places nearer the Insectivora, and in one work (**20**) puts it actually in that group. Lydekker classes all these Stonesfield Mammalia in one family, the Amphitheriidæ (including Amblotherium, Achyrodon, and Peramus); but there can be no doubt that Amphitherium should be widely separated from the triconodont group (Phascolotherium and Amphilestes). Osborn includes the latter with Triconodon and its allies in one group, the Triconodonta; Amphitherium he places with the living Polyprotodont Marsupials in the group Trituberculata, which also includes Amblotherium and its allies. Zittel adopts this arrangement, which certainly seems to be the best and safest yet proposed.

Stereognathus ooliticus, Charlesworth.

The only specimen of this interesting Multituberculate form has been purchased for the Museum of Practical Geology (London), where it now rests. This fossil, a fragment of a jaw containing three molars, came from the collection of the Rev. J. Dennis, of Bury, and was originally described by Charlesworth in 1854 (**6***a*) as a piece of the lower jaw with molars having "six similar cusps arranged in two rows" (transverse). Three years later Owen described and figured Stereognathus in detail (**21***a*). The teeth, with their three longitudinal rows of two cusps, he considers somewhat resembled those of certain Ungulata, concluding that they belonged to a "diminutive form of the great Ungulate order of Mammalia." Marsh (**12***a*) suggested that the fossil belongs to the upper jaw, as no Multituberculate teeth of the lower series are known to possess more than two longitudinal rows of cusps. The specimen is, however, too fragmentary to enable us to come to any definite opinion on this point; and its exact systematic position, therefore, must remain somewhat uncertain. It is generally classified in the family Plagiaulacidæ (**14**, **32**).[1]

[1 I take the opportunity of Mr. Goodrich's publication to record once again the existence of another Stonesfield jaw, which I obtained from a

On the Primitive Mammalian Molar.

Before closing this paper I should like to make a few remarks with regard to the "Tritubercular theory," which has been so zealously put forward by several eminent American palæontologists, and which has been so generally accepted in Europe. There are two important questions involved in the discussion: firstly as to the character of the primitive mammalian molar; secondly as to the origin and homology of the particular cusps. As before, only the teeth of the lower jaw will here be dealt with. Professor Osborn, in his illustrations of the theory of the origin of the tritubercular molar, has made large use of the Mesozoic mammals found in England; one can therefore stand on firm ground while criticising his conclusions and his interpretations of the facts.

school-fellow thirty-two years ago. I took the specimen to Professor Huxley at Jermyn Street, who cleared it from matrix and came to the conclusion that it was a second example of Stereognathus. The jaw was a fragment, but there were four molars present instead of three, the number in the type specimen. My first appearance in the field of scientific literature was as the author of a letter to the 'Geologist,' vol. iv, 1861, recording the discovery of this jaw. Much to my annoyance at the time my signature appeared as that of a Mr. E. Ray, residing at the town of Lanbeater. Whether such a town exists, or whether the name was a pure invention on the part of the printer's devil, I have never ascertained.

Further disappointment fell on me in connection with this jaw. Before Huxley had had time to figure or describe it, I took it home for a few days in order myself to make a lithograph of it. The anguish and despair of a schoolboy on finding that he had broken to powder the treasure the detection of which had been the pride of his life may be imagined. The crowns of the molars, so carefully cleared from the matrix by Huxley, were rubbed from the specimen—wrapped though it was in cotton wool—in my pocket. I carried back the now mutilated and comparatively worthless specimen to Jermyn Street, and speechless placed it in Huxley's hands, who was only a little less grieved than I was. It was put aside in some cabinet in the "den" then tenanted by the Naturalist to the Survey, and has never been seen since, though searched for some twelve years later. There is a possibility that in the course of time it may turn up either at Jermyn Street or at the College of Science, South Kensington, whither my revered friend and master—for so he became from the day when he took my Stonesfield jaw in hand—migrated in 1870.—E. Ray Lankester.]

It is well known that Osborn (16, 17), Cope (7), and other advocates of the theory assume that the primitive mammalian molar was represented by a simple "reptilian cone," the "protoconid," forming the Haplodont type of tooth. The protoconid subsequently acquired a cusp in front and behind ("paraconid" and "metaconid" respectively), giving the Triconodont type. This tooth with three cusps in a line would then have become converted into the Tritubercular type of molar by the movement outwards of the median large protoconid, and inwards of the anterior paraconid and posterior metaconid. A small posterior "heel" then became developed, which subsequently formed an external cone, the "hypoconid," and an internal cone, the "entoconid," yielding the Tritubercular sectorial type of molar seen in most orders of Mammalia.

Let us now examine the facts. If the primitive mammalian molars were simple cones, we should expect to find a gradual approximation to this condition on comparing the more specialised living mammals with the more primitive, the later fossils with the earlier. But, as a matter of fact, we find on the contrary that these simple molars are only seen in such highly modified forms as the Cetacea, and that no early mammalian fossils whatever have been yet discovered possessing them, whilst multituberculate forms increase in number the lower we search. Dromatherium and Microconodon, animals having teeth with one large and several accessory cusps, presumed to be intermediate between the Haplodont and the Triconodont types, are possibly not mammals at all, but reptiles; at all events, they differ so widely in structure from any known mammal, living or extinct, that they can afford little certain information on this question. The Reptilia themselves cannot be said to support the theory, for the most mammalian of all known reptiles, Galesaurus planiceps, has molars with three distinct cusps. On the other hand, the most reptilian of all living mammals, Ornithorhynchus, has multituberculate teeth. Dealing next with the Triconodont type of molar, we find here again that it does not occur amongst primitive forms, but in

the highly developed Carnivora, and amongst the more specialised Phocidæ. These animals possess molars of a perfect Triconodont pattern of obviously secondary origin.

Another point on which Professor Osborn lays great stress is the origin of the Tritubercular from the Triconodont type by the assumed movement outwards of the protoconid (the median cusp), the paraconid and metaconid occupying the inner angles of the "primitive triangle" so formed. Phascolotherium, Spalacotherium, and Amphitherium represent, according to that author, three stages in the process. However, I can see no traces of the beginning of such a movement in the first species. Spalacotherium has simple tritubercular molars in which the heel is not developed,[1] somewhat similar (as observed by Mr. Lydekker, 12) to those of the golden mole, Chrysochloris inaurata, and leading perhaps to the Stylodon type. As for Amphitherium, the molar shows no trace whatever of being more primitive with regard to this supposed movement of the protoconid; the heel, although not very large, is quite normally developed,[2] like that of many other Mesozoic, Tertiary, or recent forms.

The examination of existing forms only confirms these results: cusps may disappear, and cusps may arise, but the relative position of the protoconid and the two inner cusps is always essentially the same. Embryology also shows that in the development of molars the cusps arise in those positions which they will occupy in the adult tooth (Topinard, 30; Röse, 26).

Mr. W. B. Scott, in a quite recent paper (28), has clearly shown that in the premolars the protoconid remains in place while another cusp, the "deuterocone," is formed on its inner

[1] There is no evidence that the teeth of Spalacotherium are of a primitive intermediate type, even should they prove to have been evolved as suggested by Osborn. The angle of the jaw of this genus has always been described as inflected and confluent with the condyle; one specimen in the British Museum, No. 47,799, shows that it was really separate and little inflected, if at all.

[2] The small cusp figured by Osborn in the molar of Amphitherium in front of the paraconid (17) does not exist in any of the specimens.

posterior surface. So averse, however, is he to damaging Osborn's theory, that he is actually driven to the conclusion that similar cusps in precisely the same situations in the premolars and the molars are not homologous, but of entirely different origin![1]

Another argument—perhaps the strongest of all—against the assumption that the Triconodont tooth represents a stage in the evolution of the Tritubercular sectorial type is afforded by the consideration of the occurrence of the latter in the various orders of Mammalia, and the probable phylogeny of the Ditrematous mammals. That the Tritubercular sectorial type was that of the lower molars of the ancestors of all the placental mammals can scarcely be doubted in the face of the mass of evidence collected by Cope, Osborn, Schlosser, and others. All the various forms of molars met with amongst the different orders, as adaptations to special food or methods of feeding, can be referred back to this primitive type.[2] Now the Tritubercular sectorial molar occurs also amongst the Marsupials; we must, therefore, conclude that the common ancestor of both Placentals and Marsupials possessed teeth of this type; for we cannot assume without evidence that this complicated yet definite pattern arose independently in the two cases: the resemblance between the arrangement of the cusps in these teeth in the two groups is not vague and general, but definite and detailed.

We have, on the other hand, conclusive evidence that the Triconodont type of tooth has independently arisen in at least two widely separated groups, namely, the Phocidæ and Carnivora, and the carnivorous Marsupials (Phascolotherium, Thylacinus, &c.); in the former certainly, and in the latter most probably, by the reduction of the cusps of the primitively Tritubercular sectorial molar.

[1] Speaking of the Insectivora, Scott naïvely remarks that "in this group, strange to say, the oldest member yet discovered exhibits the most complicated premolar structure" (28).

[2] Dr. Forsyth Major (10) does not favour this view. However, even in the teeth he figures, traces of the Tritubercular sectorial plan may be easily detected.

The evidence is, therefore, strongly in favour of the view that the common ancestor of marsupial and placental mammals had teeth with many cusps of the Tritubercular sectorial pattern. What, then, was the pattern of the molars of the ancestors of both Monotremes and Ditremes? As yet we can give no definite answer to this question; but one thing seems extremely probable, namely, that they were of an indefinite multituberculate pattern, which gave rise, on the one hand, to the elaborate multituberculate teeth,[1] and on the other to the Tritubercular sectorial. Thus the development of two longitudinal rows of three cusps would give rise to the type of lower molar common amongst the Multituberculata; the fusion of the two anterior of these cusps or the loss of one would yield the Tritubercular sectorial tooth common amongst the Marsupials and Placentals; while the loss of the inner cusps would result in the formation of a Triconodont molar. The conclusion reached is, therefore, that the primitive mammalian molar bore a crown with several cusps.

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[1] It must not be forgotten that these teeth have only been found in forms with a reduced dentition.

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EXPLANATION OF PLATE 26,

Illustrating Mr. E. S. Goodrich's paper "On the Fossil Mammalia from the Stonesfield Slate."

Reference Letters.

a. Angle. *a. c.* Articular condyle. *c.* Canine. *c. p.* Coronoid process. *i.* incisor. *m.* Molar. *m. g.* Mylohyoid groove. *pm.* Premolar.

Fig. 1.—Left ramus of Amphitherium Prevostii, inner surface exposed. Type specimen in the Oxford Museum. × 5.

Fig. 2.—Left ramus of Amphitherium Prevostii, inner surface exposed. Second specimen in the Oxford Museum. × 5.

Fig. 3.—Right ramus of Amphitherium Oweni, outer surface exposed. Type and only specimen in the Oxford Museum. × 5.

Fig. 4.—Right ramus of Amphitherium Prevostii, inner surface exposed. In the British Museum. × 5.

Fig. 5.—Left ramus of Amphilestes Broderipii, inner surface exposed. Type specimen in the York Museum. × 5.

Fig. 5a.—Anterior portion of the same fossil seen more from above. × 5.

Fig. 6.—Left ramus of Amphilestes Broderipii, outer surface exposed. First specimen in the Oxford Museum. To facilitate comparison the figure has been reversed. × 5.

Fig. 7.—Right ramus of Amphilestes Broderipii, outer surface exposed. Second specimen in the Oxford Museum. × 5.

Fig. 8.—Left ramus of Phascolotherium Bucklandi, inner surface exposed. In the Oxford Museum. × 3.

Fig. 9.—Right ramus of Phascolotherium Bucklandi, inner surface exposed. In Mr. Parker's collection. × 3.

The lines above the figures indicate the actual length of the fossils.

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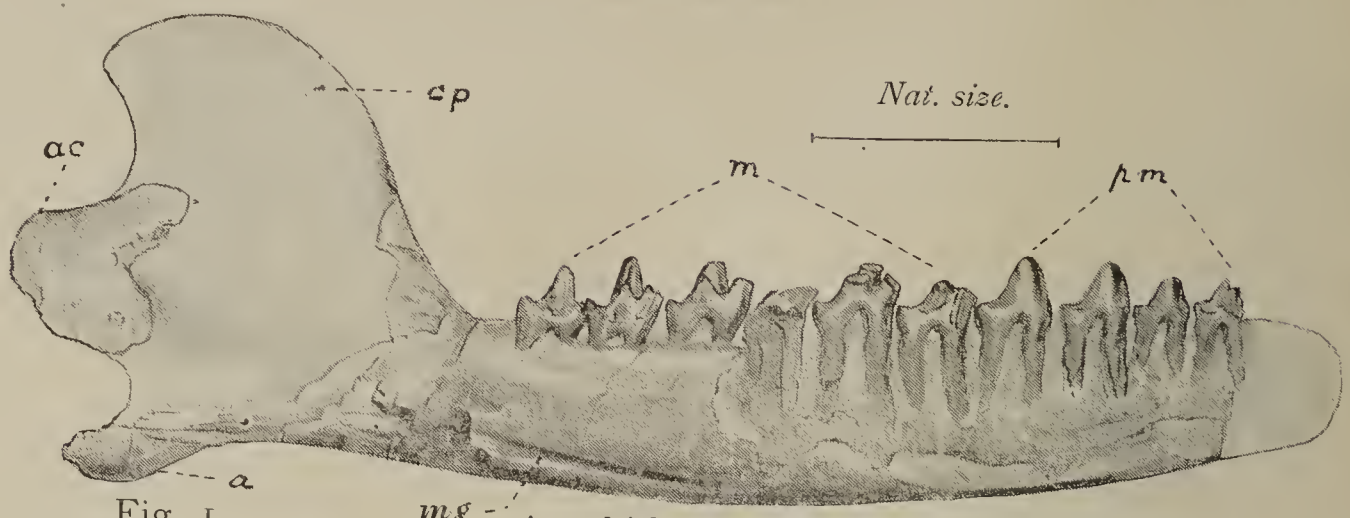


Fig. 1. Amphitherium Prevostii [Oxford Mus.].

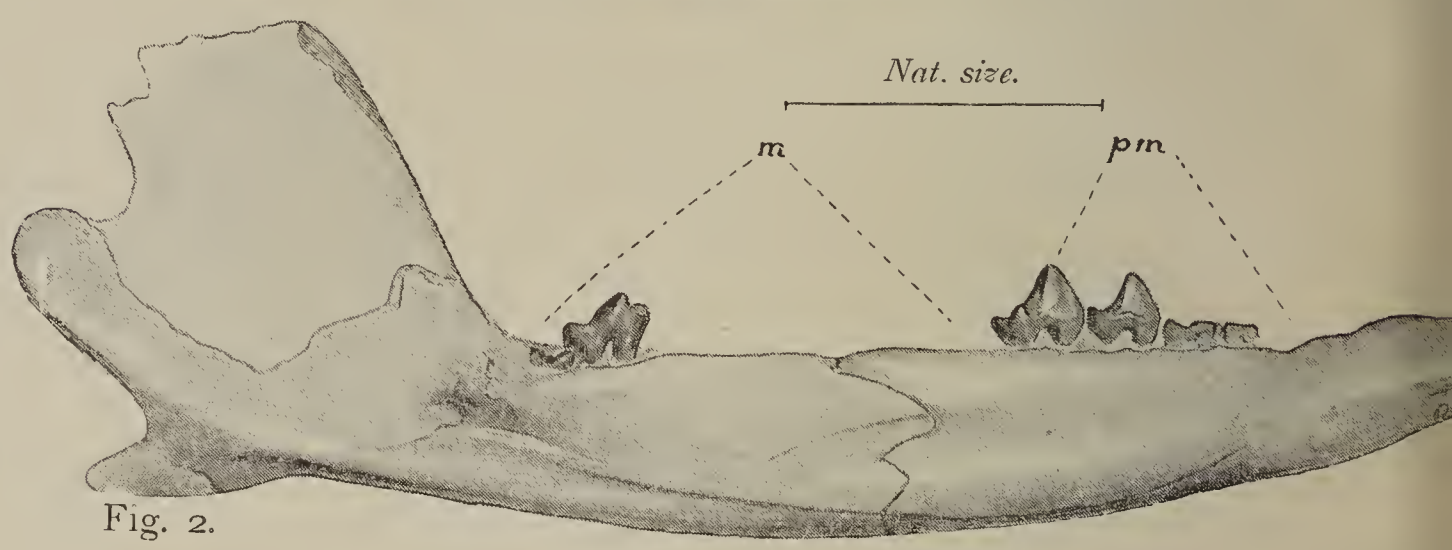


Fig. 2. A. Prevostii [Oxford Mus.].

Fig. 3. A. Oweni [Oxford Mus.].

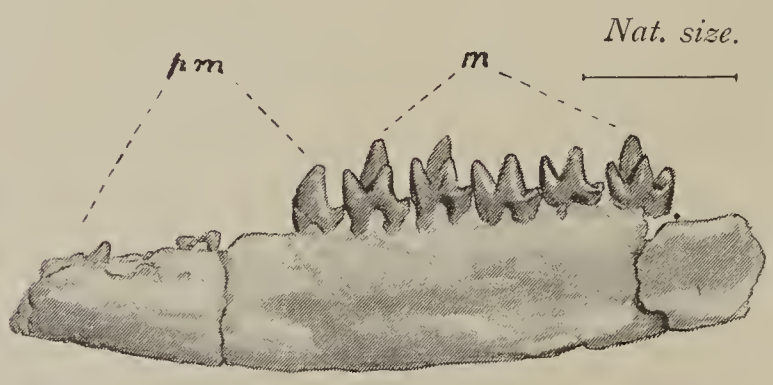
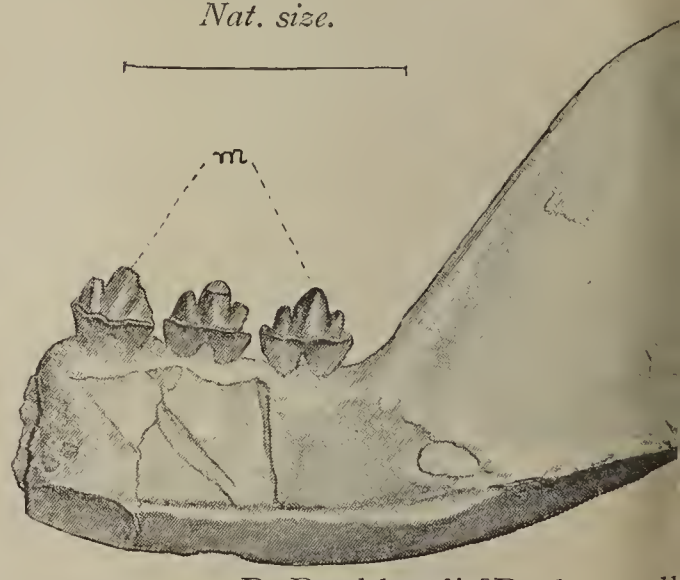


Fig. 4. A. Prevostii [Brit. Mus.].



P. Bucklandi [Parker coll

E. S. Goodrich, del.

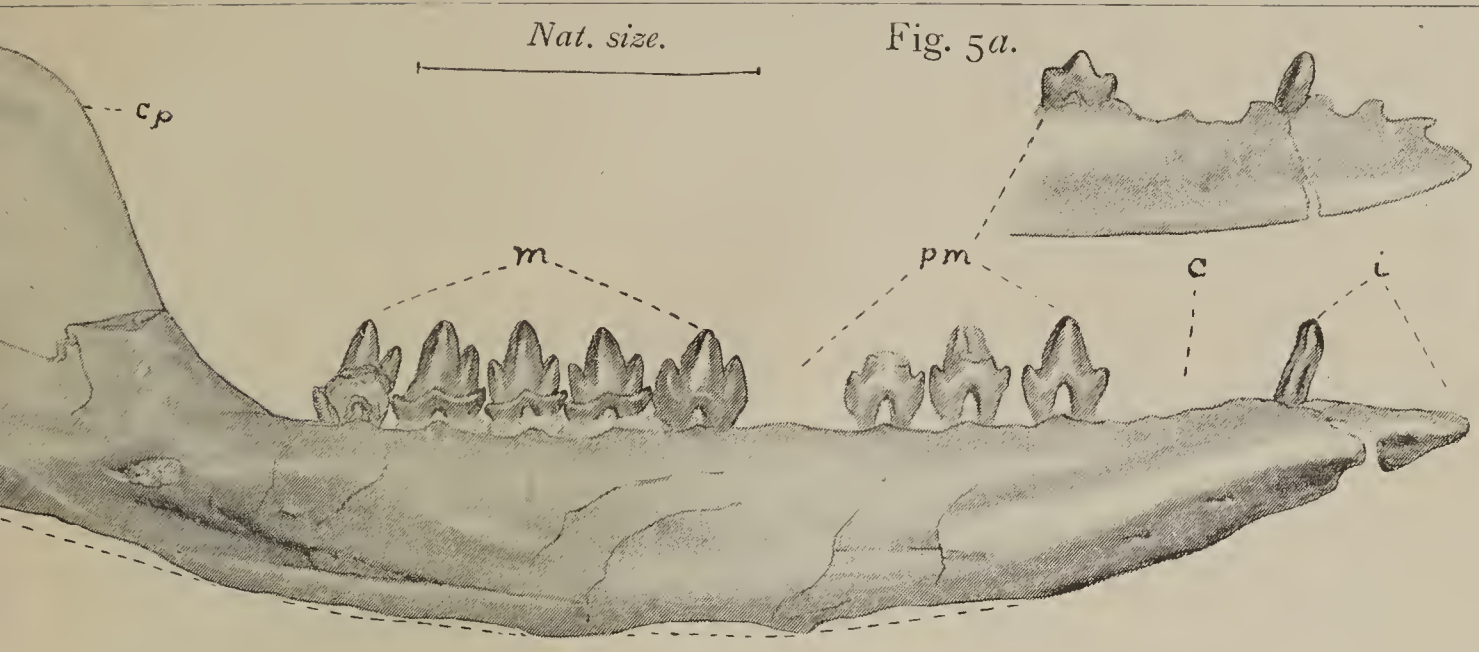


Fig. 5*a*.

Amphilestes Broderipii [York Mus.].

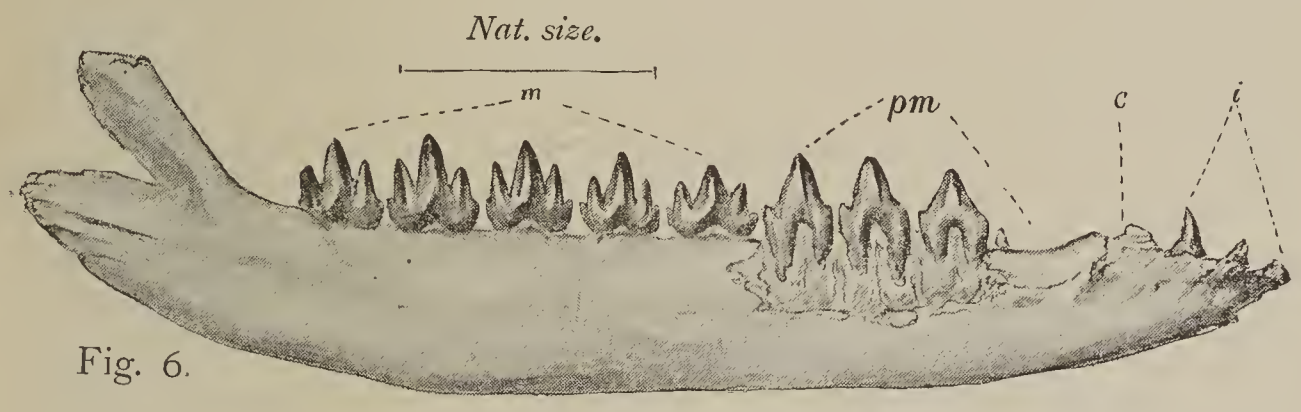


Fig. 6.

A Broderipii [Oxford Mus.].

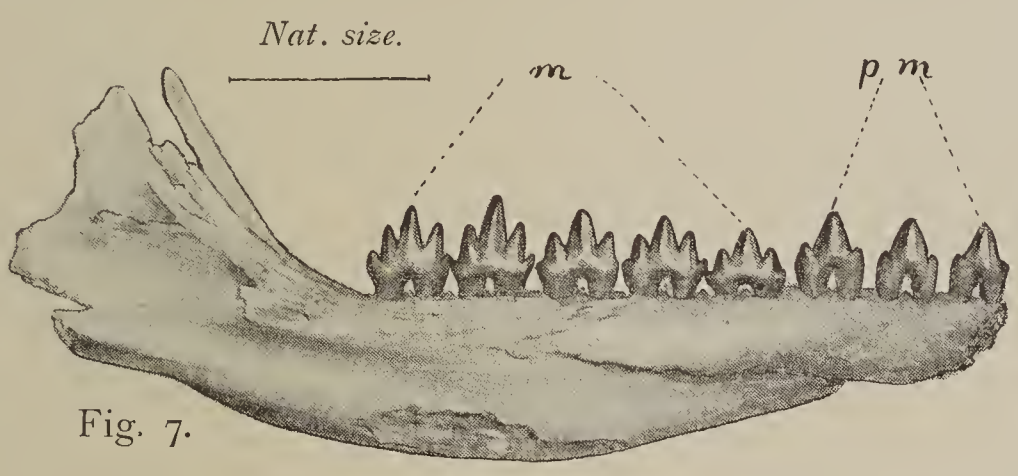
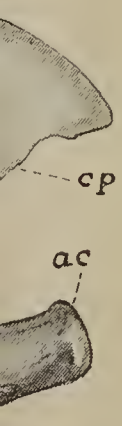


Fig. 7.

A. Broderipii [Oxford Mus.].



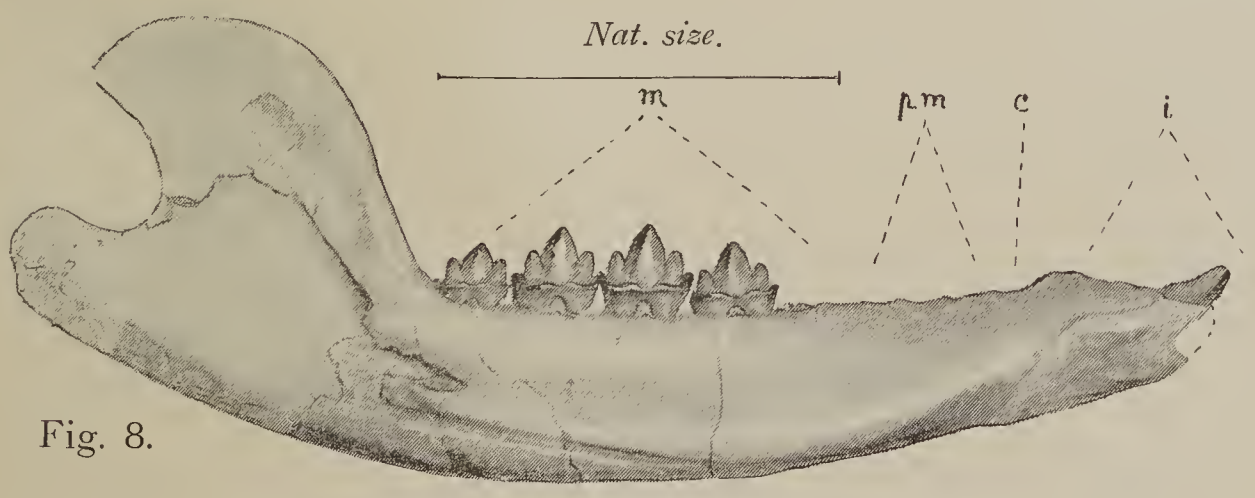


Fig. 8.

Phascolotherium Bucklandi [Oxford Mus.].